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ANNOUNCEMENT

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Malacobdella Grossa From the Pacific Coast of North America

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University of Washington

Early in the year 1924 Mr. Harvey C. McMillin called the attention of the writer to a nemertean worm inhabiting the mantle cavity of the Pacific razor clam, *Soliqua patula* Dixon. Upon investigation it was learned that the worms in question were a species of *Malacobdella*. Mr. McMillin had collected some specimens from clams in the vicinity of Copalis Beach, Washington, and at other points along the coast of Washington and Oregon. This material was turned over to the writer with some records of collection.

The question arose as to the probable injury that these worms might cause to the clams. It was with this in view that the work was first taken up. Later the identification of this form and the wide range of distribution of the single species *Malacobdella grossa* entered into the investigation and became a subject of great interest.

The writer wishes to acknowledge his indebtedness to Mr. Harvey C. McMillin for furnishing a part of the material upon which the work of this paper is based. Special thanks are due Professor J. H. Ashworth, of the University of Edinburgh, Scotland, for specimens of European species for comparative study. To Professor Trevor Kincaid, of the University of Washington, the writer expresses his appreciation for his interest and many helpful suggestions during the progress of this work.

LITERATURE

Many studies have been made upon the structure and development of *Malacobdella grossa* from European molluscs but references to it in American literature are few. Leidy (1850, 1856) seems to be the first to record it from the American clams, *Venus mercenaria* and *V. praeparca*. Verrill (1892) described two species, *Malacobdella obesa* and *M. mercenaria*, from *Mya arenaria* and *Venus mercenaria*, respectively, of the New England Coast. He stated that they were closely related to *M. grossa* of Europe and Bürger (1895) has shown their identity.

From the Pacific Coast of North America we find that this group of nemerteans is practically unknown. In a survey of the literature including the works of Griffin (1898), Coe (1901, 1904), Stimson

(1857), and Hubrecht (1887), we find no reference to the occurrence of the group *Bdellonemertea* on this coast. Coe (1905:445) mentions "a single species of this genus has been recorded from California, but it has not yet been studied sufficiently to determine whether it is identical either with *M. grossa* (Müll.) of the Eastern Coast of North America and Europe or with *M. japonica* of Japan." In another publication, Coe (1905: 306), in referring to the same instance states, "Mr. J. F. Abbott informs me that a representative of this species occurs at Pacific Grove, California. It was found by him on one occasion only, and the specimens were lost before their specific characters were determined." Thus it is evident that the *Bdellonemertea* have been unknown or only slightly known from the Pacific Coast of North America.

In Europe, *Malacobdella grossa* has been recorded from various localities by Van Beneden and Hesse (1863), Semper (1876-77), Hoffman (1877-78), von Kennel (1877-78), Bürger (1895, 1907), and others. All of the above named investigators have made more or less detailed studies of its structure and method of development. From Europe *Malacobdella grossa* has been reported from the mantle cavity of *Mya truncata* L., *M. arenaria* L., *Venus exoleta* L., *V. mercenaria* L., *Pholas crispata* L., *Cyprina islandica* L., *Cardium aculeatum* L., *Isocardia cor* L., and *Macra stultorum* L.

Two other species of *Malacobdella* have been found in the mantle cavities of molluscs from widely separated localities. Takakura (1897) described *M. japonica* Takak. from *Macra sachalinensis* Schrenk. taken on the northern coast (Kujukuri) of Japan, and Blanchard (1847) has reported a South American species, *M. auriculæ* Blanch., taken from the lung cavity of the freshwater gastropod, *Chilina dombeiana* Brug. in South Chile.

The present paper deals with specimens collected from *Soliqua patula* Dixon along the coast of Washington, principally in the vicinity of Copalis Beach. Clams from this particular region were found to be quite generally infested. On September 20, 1924, the writer visited the beach at Copalis and collected 14 clams of which 3 were parasitized, each harboring one worm. At another time 42 clams were examined and of these 7 were infested, one specimen containing 2 worms and the others one each. A further examination of 50 clams showed 30 to be infested with one worm each. McMillin (1924:30), in studying the clams in the same area, found 57 out of 65 to be infested. In this instance the clams were washed up on the beach after a storm while in the case of the writer they were dug up on the beach

at comparatively high tides. Clam fishermen and canners report infestations ranging from 25 to 75%. The latter figure seems to be a rather high estimate for ordinary collections. However, the figures given by McMillin show a higher percentage of infestation for that locality, and Kakakura (1897:105) reported a greater degree of infestation for *M. japonica*, finding 54 out of 56 clams to be parasitized.

CONTENTS OF THE INTESTINE OF MALACOBDELLA

Studies were made of the intestinal contents of a large number of worms. In some cases the intestine was removed, opened and the contents were washed out and studied microscopically, while in others they were studied in sections. Several species of diatoms and small crustacea made up the principal part of the food content of the intestines examined. No attempt was made to distinguish the species of either the diatoms or crustacea. A few protozoans—apparently ciliates—were observed in the intestines of several worms. These organisms were Paramecia-like in their appearance but were partly digested so that it was impossible to determine the species. A few organisms were present which apparently were long, slender flagellates, but specific determination was an impossibility. Certain unicellular plants were also observed in the intestinal contents but no attempt was made to identify them. From the foregoing it is evident that plankton constitutes the chief diet of *Malacobdella*. However, a few epithelial cells were observed in the intestinal contents of several worms, but no particular significance can be attributed to their presence. These cells were presumably from the exterior part of the viscera of the clam. Scrapings were made from the external epithelium in the regions occupied by the worms and comparisons of this material showed cells of a very similar nature if not identical. These cells could undoubtedly come from the external epithelium of the clam as it no doubt sloughs off from time to time. In all probability the mechanical irritation caused by the presence of the worms in the mantle cavity accelerates the growth and also the ex-foliation of the epithelial cells. Such cells were only occasionally encountered in the intestine and unquestionably form a minor and probably only an accidental portion of the diet. In one worm a few fibers were observed which bore some resemblance to the muscle fibers of the foot of the clam, although they were of a somewhat finer texture. It is a matter of conjecture as to whether this nemertean can cause enough mechanical injury to enable it to consume the muscle fibers of the clam for its food. However, if a lesion should be produced from other causes it might utilize

some of the tissues for food, but this apparently does not normally constitute its regular diet. From the studies made of the intestinal contents it is clearly shown that plankton normally comprises the principal diet of *Malacobdella*, and any other materials that might be consumed make up only a minor and probably more or less of an accidental portion.

EFFECT ON HOST

There is some question as to the amount of injury caused to the clams by the presence of *Malacobdella* in the mantle cavity or siphon. This nemertean is referred to as a parasite by Van Beneden and Hesse (1863), Semper (1877), Verrill (1892) and Bürger (1895). Von Kennel (1878:308) speaks of it as being a commensal and later (p. 358) refers to it as a semi-parasite. Bürger (1907:528), in discussing the parasitic nemerteans, considers *Malacobdella* as a commensal as it lives in the mantle cavity and there takes food which is brought in with the stream of water flowing through the siphon and mantle cavity. The nature of the food, from a study of the intestinal contents, favors the latter view that these worms are not true parasites but commensals or mess-mates. However, some epithelial cells, apparently from the external part of the viscera within the mantle cavity were found in the intestinal contents. These cells, no doubt, come from ex-foliated epithelium which in all probability was accelerated by the mechanical action caused by the presence of the worms.

In making examinations of a large number of clams no lesions were observed which could be attributed directly to the nemerteans. McMillin (1924:30) refers to the injury caused by these worms and mentions the fact that ulcers occur in various regions of the body although he does not associate the latter with the worms. Clam fishermen are of the opinion that these nemerteans are the direct cause of lesions and some even maintain that individuals harboring *Malacobdella* can be determined by certain external markings on the siphon and also on the shells. Detailed studies were made of these points in question and nothing was observed that would lead one to attribute the lesions or ulcers directly to the nemerteans inhabiting the mantle cavities. Certain of the clams studied displayed small lesions as well as peculiar white spots on the siphon and mantle and bluish-white markings on the shells but harbored no worms. Others showed all of the above mentioned markings and also were infested with *Malacobdella*. Still others possessed a worm in the mantle cavity or siphon but showed no abnormal markings or lesions on any part of the body.

A thorough study of the problem of the effects of this organism upon the host leads to the supposition that lesions or ulcers in clams should not be directly associated with this particular nemertean. This conclusion is derived from a study of its food habits and structure. It is possible, however, for the worm in the mantle cavity or siphon to produce some mechanical irritation by its presence which might bring about some indirect effects to its host, but on the whole it seems that *Malacobdella grossa* from *Soliqua patula* should be regarded as a commensal and not as a true parasite.

GENERAL APPEARANCE AND MORPHOLOGY

This nemertean occurring in the mantle cavity or siphon of *Soliqua patula* is rather inconspicuous as it is yellowish-white or even slightly pink in color. The color bears a close resemblance to that of the gills and viscera and since it lies in close contact with these structures it is often not readily recognized. Its movements are slow and leech-like, being attached by the large posterior acetabulum, it moves its anterior end slowly back and forth. When fully extended it may be rather slender with the anterior end slightly broader than the rest of the body (Fig. 2). In a contracted or slightly contracted condition the body is broader in the middle region (Fig. 1). The intestine is convoluted and can be readily distinguished through the body wall when alive. When filled with food, the folds of the intestine can be seen on the dorsal surface of the body. The ovaries (Fig. 1) in a sexually mature female, can be observed very distinctly through the dorsal wall, in fact, they may appear as numerous small pinhead-like nodules over the surface of the body lateral to the folds of the intestine. Each ovary opens directly through the body wall (Fig. 5) to the exterior, as commonly found in nemerteans. In a sexually mature female, ova in various stages of development may be observed in the ovaries. The testes (Fig. 2) in the male have the same distribution as the ovaries in the female. They are somewhat smaller and do not appear as prominently on the surface as do the ovaries. Each testis (Fig. 6) also opens directly to the exterior, and in them may be found sperm cells in various stages of development.

The external epithelium is of a low columnar type and is ciliated to some extent in certain regions but apparently not over the entire body. Beneath the epithelium is a layer of circular muscles which in turn rests upon a layer of longitudinal muscle fibers (Figs. 5, 6). The bulk of the body is made up of a mass of mesenchyma interspersed with bands of oblique muscle fibers.

There was no opportunity to make a study of the embryology and development of this form. The eggs and sperm are passed directly to the exterior where fertilization takes place in the water. Hoffman (1878) has made a thorough study of the development of *Malacobdella* and has shown it to be that of a direct type.

Except for a few points, discussed in the next section, the internal structure of the species under consideration agrees with that of *Malacobdella grossa* as described by other investigators. The mouth consists of a spacious cavity exhibiting several longitudinal folds, lined with tall columnar epithelium bearing cilia. The short, somewhat constricted esophagus opens almost immediately into the long convoluted intestine. Throughout the entire length of the intestine there is a lining of tall columnar cells which bear cilia.

RELATIONSHIP OF PACIFIC COAST SPECIES

A comparison of the Pacific Coast species with *Malacobdella grossa* of Europe, obtained from *Pholas* and *Cardium* (courtesy of Professor J. H. Ashworth, University of Edinburgh) and a study of the literature on the Japanese species, *M. japonica*, has revealed some very interesting facts. The size of the specimens at hand ranges about the same as that of those from the Atlantic Coast and Europe and also that of the Japanese species, perhaps the maximum size may be a little greater in those from the Pacific Coast. The largest individual measures 50 mm. in length and 11 mm. in breadth. However, size is a variable factor as sexually mature individuals are found having a length of less than 20 mm.

The chief points of interest revealed through this study were the structural similarities between the local form and *M. grossa* and also that of *M. japonica*. Japanese specimens were not secured for comparison but Takakura (1897:111) states "the Japanese species of *Malacobdella* mainly differs from *M. grossa* by its short rhynchocoelom, by its possessing the acetabular instead of an anal, commissure, and by some differences in the vascular system." In *M. grossa*, as shown by European writers and by the specimens at hand, the rhynchocoelom extends nearly the entire length of the proboscis. The proboscis passes to the posterior end of the body, in fact, into the area directly above the acetabulum. Takakura shows the rhynchocoelom in *M. japonica* to extend backwards from the anterior end only two-thirds the length of the body. This, of course, is a distinct difference between the two species. The specimens under observation show a somewhat intermediate condition, in this respect, between the above

species. In this case the proboscis and rhynchocoelom extend fully three-fourths of the length of the body (Fig. 2) and the proboscis ends there in the muscle bundles of the mesenchyme as shown by Takakura in *M. japonica*. This condition bears a slightly greater similarity to *M. japonica* than it does to *M. grossa*, nevertheless it tends to bring somewhat closer together the differences between these species.

Circulatory System

The blood vascular system (Fig. 3) of the present form bears distinct similarities to the conditions described by Hoffman (1877:10), Maclaren (1901:126), and Takakura (1897:108). Here again certain peculiarities occur which seem to bring closer together *M. grossa* and *M. japonica*. The vascular system consists of three vessels, one dorsal and two lateral, as observed by various investigators for the Bdellonemertea. Transverse connectives unite the lateral vessels in the anterior region and in the posterior region the laterals are joined by two branches of the dorsal vessel (Fig. 4). The dorsal vessel arises anteriorly, slightly behind the commissures of the brain, by the union of two branches from the lateral vessels. At intervals along both dorsal and lateral vessels small branches are given off, the most of which are short and simply supply the tissues in the immediate vicinity of the main vessels. Others are longer, extending to greater distances and some even fuse with similar branches from the other main vessels, thus forming an anastomosing network, principally in the middle region of the body. The anastomosis is less complicated than that shown for *M. japonica* but more so than occurring in *M. grossa*. The many short branches given off from the three main vessels almost perfectly resemble those of the European specimens at hand. In the posterior region of the body the lateral vessels bend mesiad to points ventral to the intestine, then turn lateral again through a somewhat winding course until reaching the outer margins of the nerve cords. Here they ascend above the cord and bend inward again, passing slightly forward to the median line where they fuse with the dorsal vessel (Fig. 4). Small branches are given off at intervals from the vessels to supply the tissues in the posterior extremity of the body. This condition is almost identical with that found in *M. japonica* by Takakura. In *M. grossa* (Fig. 3) the main vessels do not extend as far posteriorly and there are longer, more complicated, branches passing to the posterior extremity and into the acetabulum where they form a network. On the whole the structure and arrangement of the blood vascular system is very similar to that of *M. japonica*, especially in the posterior re-

gion. However, there are likenesses to both forms since the middle region bears a striking resemblance to *M. grossa*.

Excretory System

The excretory system is similar in all respects to that found in both the European and Japanese forms. Takakura regarded this system as being very nearly identical for the two species.

Nervous System

The nervous system is typically that of *Malacobdella grossa*. The brain is composed of two lateral ganglia connected by two commissures, one dorsal and the other ventral to the proboscis (Figs. 7, 8). Lateral nerve stems pass posteriorly extending to the region of the acetabulum where they follow a somewhat winding course and unite in front of the anus, thus forming the anal commissure (Fig. 4). In the region of the acetabulum the lateral nerves become somewhat thickened but as they extend mesiad and approach the anal region they become somewhat reduced again into the slender commissure. From the thickened areas, or masses of ganglionic cells, arise small nerve fibers which supply the acetabulum. This thickening of the lateral nerves is in accord with the condition described by Von Kennel (1878) for *M. grossa* and also agrees with that found by Takakura (1897) in *M. japonica*. The anal commissure is distinctly a characteristic of *M. grossa*. In this respect, the Japanese species displays a marked difference in that the commissure is wholly behind the anus and lies in or very near the acetabulum.

DISCUSSION

From the foregoing it is evident that the present species is similar in many respects to both *Malacobdella grossa* and *M. japonica*. The size, external appearance, and activities are very nearly identical, perhaps the Pacific Coast form may reach a slightly greater maximum size, but that can probably be accounted for by inhabiting a different host. Such structures as the mouth, alimentary canal, reproductive organs, and excretory system show no differences. The external epithelium with its glands, musculature, mesenchyme, and epithelium of the alimentary canal appear alike. The points, mentioned elsewhere, that distinguish the Japanese species from *M. grossa* are, the short rhynchocoelom, blood vascular system and the acetabular commissure. In the form here under discussion the length of the rhynchocoelom

bears a close resemblance to that of *M. japonica*, however, it is somewhat longer but not reaching the extreme length revealed in *M. grossa*. This arrangement of the rhynchocoelom places it in an intermediate position between the two species.

The circulatory system to a large degree is also that of *M. japonica* with some modifications showing distinct relationship to *M. grossa*. This arrangement of the rhynchocoelom places it in an intermediate position between the two species.

The circulatory system to a large degree is also that of *M. japonica* with some modifications showing distinct relationship to *M. grossa*. In the posterior region the anastomoses are almost typical of the Japanese species while in the middle region it manifests distinct resemblance to that of the Atlantic Coast and European forms. MacLaren (1901:126) states "so many discrepancies exist in descriptions of the blood vessels of this animal, that one must needs believe that the species varies largely in different localities. Certainly my specimens differ considerably from those described by Oudemans, Bürger and V. Kennel, and the peculiarities were constant in the very large number of specimens examined." This would lead one to disregard the blood vascular system as a basis for the classification of the Bdellonemertea.

Finally, in the consideration of the nervous system we find one that is typical for *Malacobdella grossa* as it possesses a distinct anal commissure and not the acetabular type found in *M. japonica*. Thus, one is confronted with a peculiar problem as this form bears marked resemblance to both species and at the same time presents certain differences. On the whole, after a consideration of the facts obtained it is not deemed advisable to establish a separate species for the present form. The accumulated facts bear evidence of a situation which distinctly lessens the differences between *Malacobdella grossa* and *M. japonica*.

A survey of the above points shows rather clearly that the present form should be known as *Malacobdella grossa* (Müller). This conclusion was derived chiefly on the basis of the nervous system. The rhynchocoelom is no doubt subject to variation and in this instance is not a factor of sufficient importance to warrant its designation as a specific character. A review of the vascular system shows it to be subject to such modifications that it can well be disregarded in the discrimination of this species. The nervous system is generally regarded as being more conservative and hence subject to less modification.

It was impossible to secure specimens of *M. japonica* for comparison but unquestionably that species should stand, at least for the present, or until further comparative studies can be made of these forms. No doubt further studies would reveal some interesting facts concerning comparative structures of these forms.

This study adds a new host and a new locality to the wide distribution of *M. grossa* as shown by the work of Bürger (1907:529) for this parasitic nemertean.

SUMMARY

1. The presence of *Malacobdella grossa* (Müller) is recorded from the Pacific Coast razor clam, *Soliqua patula* Dixon, on the coast of Washington and Oregon.

2. The food of *Malacobdella grossa* is almost wholly plankton but some exfoliated epithelial cells apparently from the visceral region within the mantle cavity may occasionally be consumed.

3. Injury to the clam, if any, is probably of a minor nature and is no doubt chiefly mechanical.

4. The species of *Malacobdella* on the Pacific Coast resembles *M. japonica* Takak. in having a shorter rhynchocoelom than *M. grossa* (Müller) and also in the arrangement of the posterior part of the blood vascular system.

5. There is a resemblance to *M. grossa* of the Atlantic Coast and Europe by having an anal commissure in the nervous system which is typical for that species and also by the arrangement of the circulatory system in the middle region of the body.

6. The species studied in this paper is regarded as *M. grossa* mainly upon the consideration of its nervous system. It shows a distinct relationship to *M. japonica* and the facts revealed here clearly indicate a closer affiliation than has been regarded heretofore.

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PLATE 1

<i>a</i> — acetabulum	<i>lm</i> — longitudinal muscle layer
<i>an</i> — anus	<i>ln</i> — lateral nerve
<i>ac</i> — anal commissure	<i>lv</i> — lateral vessel
<i>b</i> — brain	<i>n</i> — nerve branches
<i>c</i> — circular muscle layer	<i>o</i> — ovary
<i>dc</i> — dorsal commissure	<i>p</i> — proboscis
<i>dv</i> — dorsal vessel	<i>r</i> — rhynchocoelom
<i>e</i> — epithelium	<i>T</i> — testes
<i>es</i> — esophagus	<i>V</i> — ventral commissure
<i>i</i> — intestine	

All drawings were made with the aid of a camera lucida.

1. Mature female of *Malacobdella grossa*, x 3.
2. Small male, mature, *M. grossa*, x 3.
3. Vascular system in posterior portion of *Malacobdella grossa* of Europe (after Bürger).
4. Partial reconstruction of posterior end of *M. grossa* of Pacific Coast, x 20.
5. Section through mature ovary taken from longitudinal section of *M. grossa*, x 125.
6. Section through testis from longitudinal section, *M. grossa*, x 125.
7. Cross section through brain and anterior commissure. Semidiagrammatic, x 20.
8. Partial reconstruction of anterior end. Semidiagrammatic, x 20.

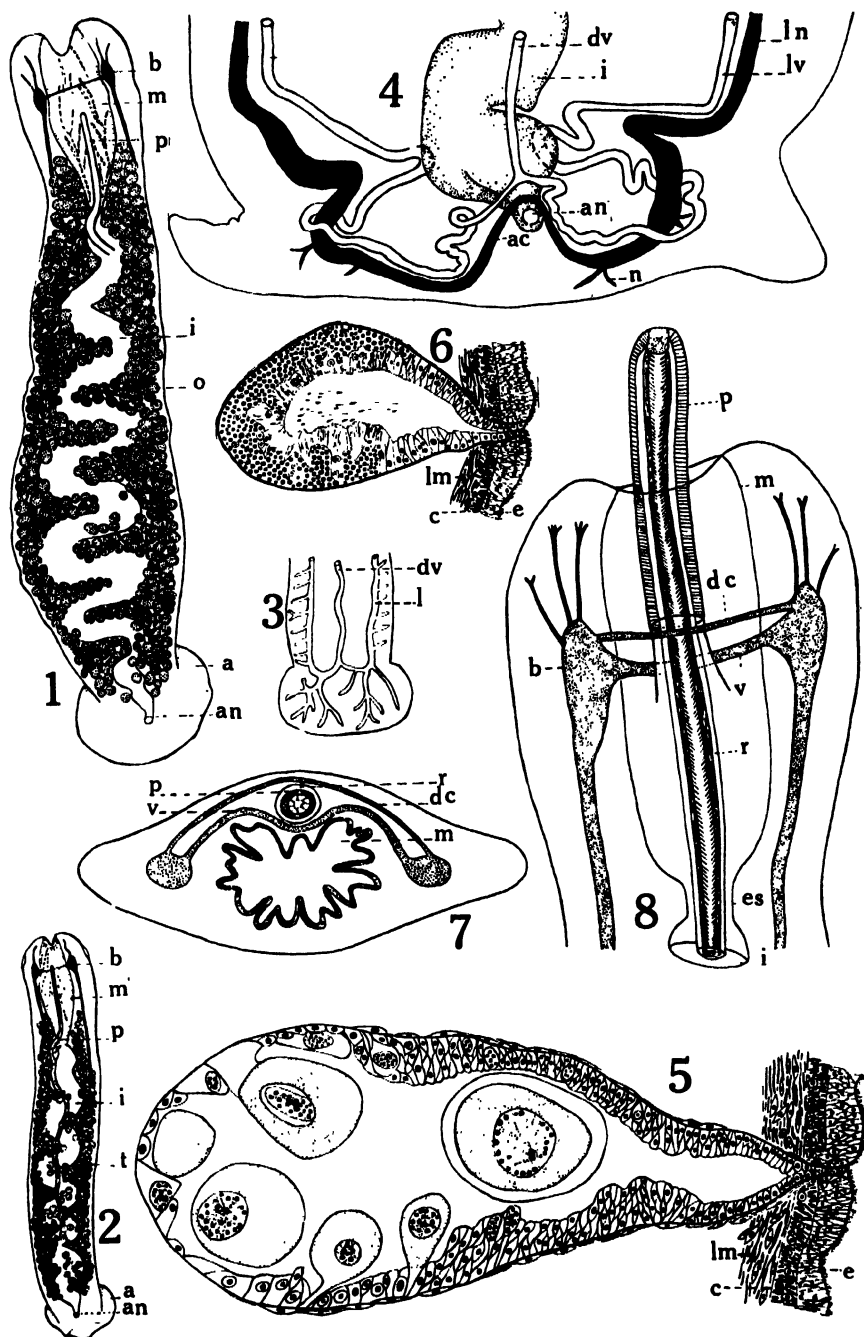


PLATE 1

Notes on Certain Bryozoa in the Collection of the University of Washington

CHAS. H. O'DONOGHUE, *D.Sc.; F.Z.S.; F.R.S.C.*

University of Manitoba, Winnipeg

To aid us in our studies of the Bryozoa of the Vancouver Island region, Professor Trevor Kincaid very generously placed at our disposal the collection of these animals in the University of Washington. Many of them were collected in and around San Juan Island or in the waters of Puget Sound and these have been dealt with in a separate note. A few however came from Alaska or from California and among these we have considered the following as worthy of remark. Three of the species have not been recorded previously from the Pacific Coast of North America and the genera to which two of them belong are also new to that area. Three others are apparently new to science. In view of our somewhat limited knowledge of this group on the coast we think they should be placed on record and at the same time we desire to tender our best thanks to Professor Kincaid.

We also desire to thank the Biological Board of Canada without whose assistance the work would not have been done and Dr. W. C. Clemens, Director of the Biological Station, Namaino, where part of the investigation was carried out.

This does not appear a fitting place to enter into the vexed questions of classification and so we shall pass straight to a consideration of the specimens.

BRYOZOA Ehrenberg 1831

Sub-class ECTOPROCTA Nitsche 1869

Super-order GYMNOLEAETA Allman 1856

Order CTENOSTOMATA Busk 1852

Family FLUSTRELLIDAE Hincks 1880

FLUSTRELLA Gray 1848. Genotype, *Flustrella hispida* Fabricius 1870. *Flustrella corniculata* (Smitt), as *Alcyonidium corniculatum* in Oerstedt af. Kongl. Vetenskapsakad. Forh. 1871:1123-1124, pl. 20, figs. 10-16, 1871.

The zoarium is in the form of a fairly thick gelatinous encrustation growing over various algae and it is characterized by bearing a large number of horny spines both simple and branched. The individ-

ual zooecium is generally of an elongated hexagonal shape but at the growing edge the walls are curved instead of being more or less straight. The surface is slightly convex and the division lines between the zooecia are clearly marked. In dried material the frontal wall sinks in and leaves quite a well marked margin around the zooecium. The orifice when partially extruded is in the form of a raised, transverse, narrow opening guarded by two lips the lower of which is strengthened by what appears to be a chitinous border. When the orifice is closed however it is hardly discernible in living or wet specimens and so its characteristic structure is easily overlooked. Each zooecium is furnished with a number of spines which exhibit a considerable range of variation. There may be, particularly in younger zooecia, one or two simple spines near the anterior end or again the whole margin may be furnished with a considerable number of these structures. All these may be simple spines and so we have a condition resembling *F. hispida* or some or all of them may be branched or bifurcated and branched. In some parts of the present, dried specimens, the spines are so plentiful and so branched that the actual surface of the zooecia is practically invisible. The polyps were naturally not present so that the number of their tentacles could not be ascertained.

Locality. The material bears the label "St. Paul Island" with no data but was presumably collected between tide marks.

Notes. The examination of the present material raised two interesting points which cannot be settled without further investigation. The first is, that preserved material in its young stages when only a few simple spines are present, is practically indistinguishable from *E. hispida* (Fabricius). The second is that it appears quite probable that at any rate some of the material described as *Alcyonidium cervicorne* Robertson (Proc. Wash. Acad. Sci. II:330, 1900) and *Alcyonidium spinifera* O'Donoghue & O'Donoghue (Cont. Canadian Biol., N.S., I:50, 1923) is referable to this species. It is the first time the genus or species has been recorded from this coast.

Family VESICULARIIDAE Hincks 1880

AMATHIA Lamouroux 1812. Genotype, *Amathia lendigera* (Linne), *Sertularia lendigera* Linne 1758.

Amathia distans Busk, in Reports Challenger Exped. Zool. XVII:33, pl. VII, fig. 1, 1886.

The zoarium is in the form of a tangled mass of brown filaments .12-.15 mm in diameter which when examined closely are seen to be dichotomously branched. A filament is composed of a number of

long straight segments separated by partitions; these are sometimes referred to as internodes and nodes respectively. Each internode is provided with a spirally arranged band of zooecia situated distally and occupying not more than half its length, leaving the lower half bare. The band consists of ovoid or oblong zooecia .1-.18 mm long, distinct from one another but closely apposed and generally arranged in a double row although they may be three abreast. Each zooecium has a cylindrical base and a bluntly conical terminal portion which may be much contracted.

Locality. The material bears the label "La Jolla, rocks near Station."

Notes. There seems little doubt that this is the same species, that was described by Busk as *A. distans* and is an interesting record since he found it in material from Bahia dredged in 18-37 meters. It is the first time that this species or genus has been recorded from the Pacific Coast of North America.

Order CHEILOSTOMATA Busk

Sub-order ANASCA Levinsen

Division MALACOSTEGA Levinsen 1909

Family BICELLARIIDAE Smitt 1867

BUGULA Oken 1815. Genotype, *Bugula neritina* (Linne), *Sertularia neritina* Linne 1758.

Bugula pedunculata sp. nov.

The zoarium is in the form of small branched stocks growing upon a frond of alga to which they are attached by rooting fibres. None of the pieces branch more than three times. The distal ends of the individual zooecia are boat-shaped but they have a much longer basal portion than in many members of the genus, recalling the condition in *B. longissima* Busk (Chall. Rep. X:42, pl. XXXI, fig. 7, 1884). The aperture does not occupy more than half the length of the zooecium and bears two bluntly pointed processes at its upper corners. The narrow basal portion passes along the side of that part of the zooecium below, that bears the aperture, and so the whole branch appears slender. Each zooecium, save the first of a new branch, has an avicularium. This is a small, globular structure with a curved beak and mandible and it is borne upon a short curved stalk. The stalk arises from the base of the narrow end of the zooecium immediately above the top of the aperture of the next zooecium below on the same side. At first sight it almost looks as if the avicularium

arises from the top of a zooecium but closer examination shows the condition to be just as described.

Where a branch is produced one zooecium bends sharply away from the next below it on the other side, near the top of the aperture of the latter. The first zooecium of the branch grows in the axil between these two and almost immediately enlarges to form the aperture-bearing portion. Thus this zooecium, the initial one of the branch, differs from the remainder in having a very short base upon which there is no avicularium.

The oecium is in the form of a hollow ovoid with an oval opening directed postero-laterally. It is pedunculate and the stalk arises from a tiny, flattened, circular chamber which lies on the mesial side of a zooecium near the top of the aperture. Apparently it is commonly produced upon the zooecium just before a branch.

Locality. The label attached bears the inscription "La Jolla, rocks near Station," but no other data.

Notes. The present species recalls *B. neritina* in having a pedunculate oecium, these being the only two members of the genus from the coast with this. The differences however are quite marked, *B. neritina* possessing no avicularia whereas they are always to be found in the present form. Yet again the zooecia of *B. neritina* do not possess an elongated basal portion. The form appears to be new and we suggest the name *Bugula pedunculata* to call attention to the pedunculate oecium.

Bugula multiseriata sp. nov.

The zoarium forms conspicuous tufts that may reach a height of from 5-6 cm, and they are attached to the substratum by a bundle of coarse rooting fibres springing from the lowermost zooecia. The colony is composed of 8-14 broad leaf-like lamellae with a spiral arrangement. A wide lamina may contain 36-40 zooecia in a transverse row.

The zooecium is elongate, deep and boat-shaped with the margin projecting. The top edge is generally rounded or it may bear a corner at one or both sides or this corner may be produced into a short but distinct spine. The zooecia are arranged fairly regularly in alternate rows and one arises from the other on the dorsal side by a quite straight transverse joint with no sign of the tongue-like projection that is found in forms like *B. turbinata*. The mouth is a somewhat flattened curve of less than a semicircle. Avicularia are present in varying numbers in different parts of the colony. Sometimes one is borne near the lower corner of each marginal zooecium but these may

be absent. Yet again they may be developed on a number of zooecia in the central region of the leaf or none may be present there. The marginal avicularia are slightly larger than the ones on the blade of the leaf. Each avicularium is joined to the margin of the aperture of the zooecium near the lower end by a very short stalk. It is a fairly large globular structure with a short stout beak curved over at the tip. To a certain extent it recalls the avicularium of *B. turbinata* but the type of the colony, the size of the zooecia, the kind of junction between the dorsal surfaces, etc., are quite different.

The ooecium is a large, extremely prominent structure which overhangs the front end of the zooecium and covers a large part of the aperture of the zooecium in front. It is composed of an ect-ooecium and an endooecium, the latter being marked by faint radiating lines. If spines are present on the zooecium they are not hidden by the ooecium but stand up at its lower lateral corners. In those places where the zooecia are tightly packed, and ooecia and avicularia plentifully developed, the colony presents a very striking appearance and the zooecia themselves are almost entirely hidden.

Locality. The specimens came from St. Paul Island, Alaska, but the label gives no information as to depth.

Notes. This is a very striking species and apparently a new one. The name *Bugula multiseriata* is proposed to call attention to the many rows of zooecia in a leaf.

Sub-order ASCOPHORA Levinsen 1909

Family ESCHARELLIDAE Levinsen 1909

LEPRALIA Johnston 1847.

Lepralia pallasiana (Moll.), as *Eschara pallasiana*, Seerinde, p. 64, pl. iii, fig. 13, 1803. Hincks, Brit. Marine Polyzoa, p. 297, pl. 33, figs. 1-3 and pl. 24, fig. 4, 1880. Osborn, Bryozoa Woods Hole Region; Bull. U.S. Bur. Fish. XXX:240, pl. XXV, fig. 54 and pl. XXX, fig. 89, 1910.

The zoarium is encrusting and forms a yellowish white layer with a distinctly and fairly regularly patterned surface owing to the fact that the zooecia are arranged in rows.

The zooecium is large and oblong, and generally just over twice as long as broad. The frontal is perforated by a number of large holes so that it appears as a reticulum. It is covered with a hyaline epitheca upon which a black line indicates the line of demarkation between the zooecia. The aperture is slightly higher than broad; its upper margin is deeply arched and the lower margin straight or slightly curved outwards. There is a slight constriction near the pos-

terior margin. The border of the aperture is quite thick and in the middle line below it is produced into a very prominent, pointed mucro which is so long in some cases that it appears as a spine.

No avicularia or oecia were found on any of the specimens.

Locality. The present material was obtained at Homer, Alaska, but no information as to depth is available.

Notes. This species offers a considerable range of variation in the presence or absence of the spine-like mucro, the presence or absence of avicularia, the extent of development of the margin of the aperture, etc. Several of these varieties are well shown in Hincks' illustrations, and our own material, while not quite like any of them, is more like some of them than Osborn's variety. In the latter the perforated frontal extends all round the aperture, a feature not found in any of Hincks' varieties nor in our own. We have little doubt that the present material is referable to this species and have provided an illustration for the purposes of comparison since it is the first time this species has been recorded from the Pacific Coast of North America.

Family SMITTINIDÆ Levinsen 1909

PORELLA Gray 1848. Genotype, *Porella cervicornis* (Pallas), *Millepora cervicornis* Pallas 1766.

In Hincks' definition of this genus (Brit. Marine Polyzoa, p. 320, 1880) he states that the foliaceous forms are composed of a single layer of cells. While this is true of the British forms, Canu & Bassler (Bull. U.S. Nat. Mus. No. 106:485-, 1920) include a number of bilamellar species. Again, it happens that the British forms do not have adventitious avicularia; such however are present in some species listed in Canu & Bassler. The definition of the genus should be amended to include these possibilities.

Porella pacifica sp. nov.

The zoarium may possibly form a thick encrustation or, as in most of the specimens examined, a stout bilamellar expansion. No complete colony was available but pieces 15 mm square obviously form part of a considerably larger colony and are 1.5 mm thick. The surface of the older parts of the zoarium appears to the naked eye as a smooth surface perforated by a series of pores.

The young zooecia are elongated and roughly rectangular with curved long sides. They are surrounded by a row of small areolations and separated from one another by a low but distinct partition. The primary aperture is little more than a semicircle, rounded above and

straight below with slightly rounded corners. The hinder end of the frontal is fairly smooth and bears a series of faint radiating lines. The front part, not quite half the total length, is occupied by the avicularian chamber which does not project much but passes fairly deeply into the zooecium. The avicularium is always situated nearer one side, never exactly median, and its semicircular mandible is directed postero-mesially at an angle of about 45-60 degrees to the hinder end of the aperture.

With increase of age and calcification the demarkation between the zooecia becomes less distinct and finally disappears. A peristomice and somewhat pyriform secondary aperture are produced, within which the avicularium is situated. Here and there the aperture seems to be closed in altogether leaving only the avicularium to mark its former position. In the older parts of the colony two different types of adventitious avicularia are produced. The first is a large, spatulate avicularium occurring occasionally over the zoarium, the mandible of which closes into a raised rim. This is borne on a chamber that appears as a low oval prominence, but when its front is broken it will be seen to be quite a deep cavity. The second is a somewhat similar but smaller type of avicularium that is found in the region of the ooecia. These are more plentifully produced and sometimes are to be found one by each side of an ooecium near its opening.

The ooecium is a well marked, prominent, globular structure composed of distinct ectooecium and endooecium. It opens into the peristomice above the operculum. The front of the ooecium bears a series of pores characteristically arranged in the form of an elongated rosette.

Locality. These specimens are simply labelled "Albatross. N. W. Pacific" with no further data.

Notes. This is an interesting form in several respects. All the previous members of the genus recorded from either coast of North America are encrusting whereas this is bilamellar. None of the forms previously recorded from Pacific North America have adventitious avicularia. The most usual position for the typical avicularium beneath the aperture is in the middle line with the mandible pointing downwards whereas here, as noted, it is slightly lateral.

No similar form has been found described and if it is new as seems probable the name *Porella pacifica* is suggested.

PLATE 2

FIG. 1. *Flustrella corniculata*; part of a colony near the growing edge showing young zooecia; *L*, lower lip of orifice; *O*, orifice; *P*, intercostal partition; *S*, spine. $\times 39$.

FIG. 2. *Amathia distans*; part of a zoarium with the ends of the two lateral branches; *B*, branch; *I*, internode; *Z*, spiral of zooecia. $\times 24$

FIG. 3. *Bugula pedunculata* sp. nov.; part of a zoarium showing branching; *A*, avicularium; *Ap*, aperture; *M*, mandible; *S*, stalk of avicularium. $\times 29$

FIG. 4. *Bugula pedunculata* sp. nov.; part of a zoarium with a pedunculate ooecium; *A*, aperture of zooecium seen through the latter; *O*, ooecium. $\times 39$

FIG. 5. *Bugula multiseriata* sp. nov.; portion of the edge of a frond; *A*, avicularium; *O*, ooecium; *Op*, operculum; *S*, spine. $\times 26$

FIG. 6. *Lepralia pallasiana*; part of a zoarium; *A*, aperture; *B*, thickened border; *M*, mucro. $\times 24$

FIG. 7. *Porella pacifica* sp. nov.; part of a zoarium showing young zooecia near a growing edge; *A*, avicularium; *AC*, avicularian chamber; *Ap*, primary aperture; *P*, interzooecial partition. $\times 24$

FIG. 8. *Porella pacifica* sp. nov.; part of older region of zoarium showing secondary apertures, adventitious avicularia and ooecia; *A*, avicularium; *O*, ooecium; *SA*, secondary aperture. $\times 24$

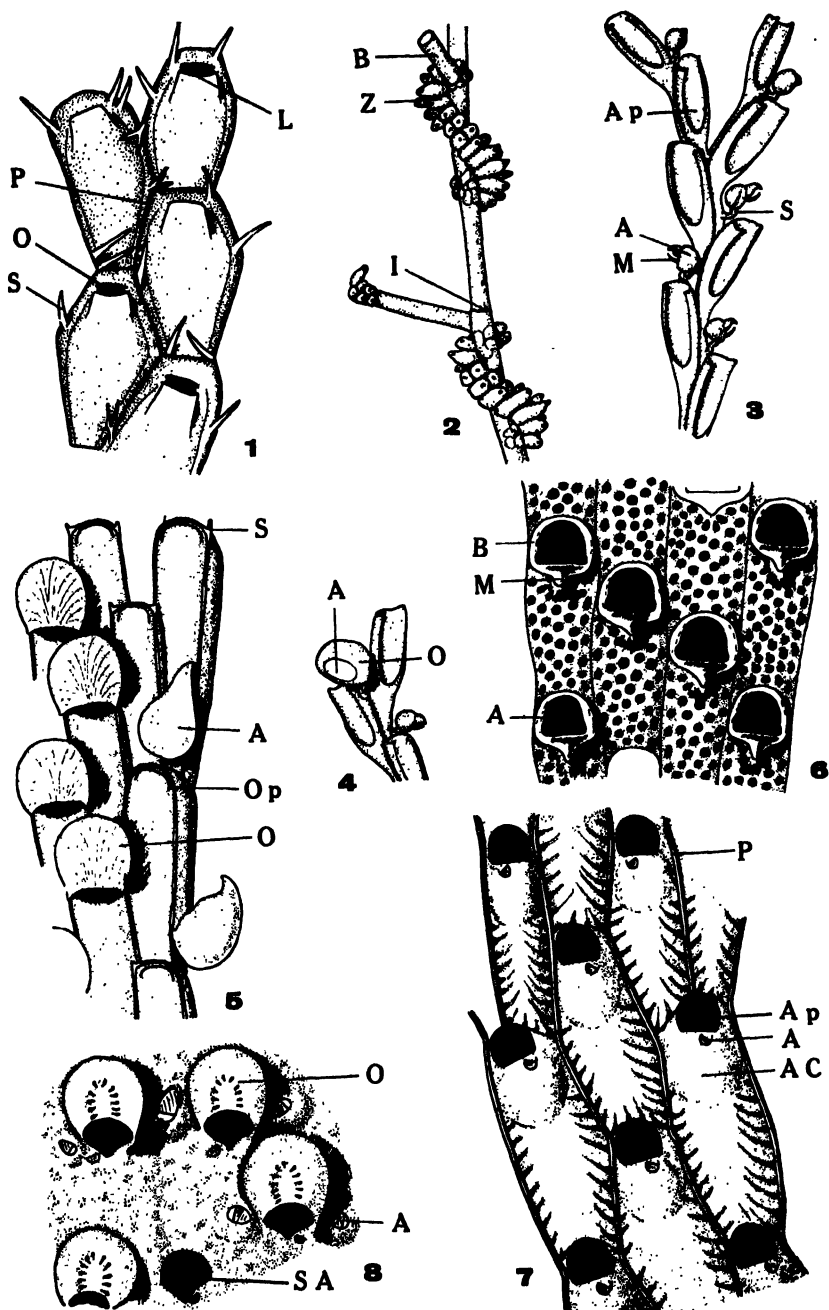


PLATE 2

Animals Living on Kelp

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During the summer of 1922 the following beds of the large bulb kelp, *Nereocystis luetkeana*, were studied to determine what animals inhabit these plants: the buoy between Shaw and Brown Islands; northeast point of Turn Island; southwest point on Shaw Island; two beds near entrance of Kanaka Bay; Madrona Point; Point Caution; Cattle Point; beds near Argyle Bay; northeast point of Brown Island. These areas are shown covered with small circles in a paper by Shelford & Towler.* These particular beds were selected for their convenience for study, differences in depth, movement of water and character of bottom.

In observing the fauna, the laminae or fronds, the stipe or stem, and the holdfast of the kelp were considered separately. The laminae were first studied from a row boat, but more accurate work could be done by cutting the stipe just below the pneumatocyst and placing the laminae in a tub. In this way both dorsal and ventral surfaces could be examined and an accurate count made of the animals. The holdfasts were pulled from the rocks and carried to the laboratory for study.

The fauna of the laminae includes the following: *Lacuna porrecta* Carp. (snail), numerous in quiet water; *Lacuna unifasciata* Carp. (snail); eggs of *Lacuna* (snail), numerous in shallow quiet water; *Epialtus productus* Rand. (crab); *Caprella*, numerous in shallow water; Amphipods; *Pentidotea rotundata* (Isopod); Bryozoa, found on stems and laminae.

The stipe does not support many animals. Snails and amphipods were the only forms found in very great numbers. Patches of Bryozoa and *Lacuna* eggs were plentiful in comparatively shallow water.

The fauna of the holdfasts includes upward of 40 species. Nine holdfasts from each of the beds studied disclosed 2605 individuals.

*Animal communities of the San Juan channel and adjacent areas. Publ. Puget Sound Biol. Sta. 5:33-73, 1925.

TABLE 1. Showing the distribution of animals in the various areas studied. Numbers in the body of the table indicate the number of individuals taken from nine holdfasts in each locality.

A—Buoy G—Argyle gr—gravel rock
 B—Turn Island H—Point Caution sw—swift
 C—Shaw Island I—Madrona Point sc—slight current
 D—Kanaka Bay, East J—Kanaka Bay, West q—quiet
 E—Cattle Point r—rock m—moderate
 F—Brown's Island sr—small rock sl—slow

Lettered localities.....	A	B	C	D	E	F	G	H	I	J
Bottom.....	r	r	r	r	r	sr	r	gr	r	sr
Current.....	sw	sw	sw	sw	sw	sc	q	m	m	sl
Average depth in meters.....	10	10	10	10	10	10	10	5	4	4
pH.....	7.8	7.8	8	7.9	7.8	7.5	7.8	7.7	7.9	7.6
Amphiporus bimaculatus Coe.....	6	6	1	4	8			11		
Ophiopholis aculeata Gray.....	62	30	38	3	140		2	13		
Nudibranchs (unidentified).....	1								1	
Amphipods (unidentified).....	30		5	612	9	52	18	45	353	328
Nereis virens Sars.....	2	15	4	11	37	34	12	45	0	15
Harmothoe imbricata L.....	12	6	1	6	18	25	3	45	5	5
Nereis agassizi Ehl.....	6	0	0	37	51	9	6	76	5	75
Lacuna porrecta Carp.....		2			6	21		17	30	
*Pecten hindsii Carp.....		1							1	
Caprella sp.....		8			1				1	2
Serpulids (unidentified).....		4								1
Lepidochitona lineata Wood.....			1							
*Strongylocentrotus drobachiensis Ag..			2					1		
Cardium californiense Des.....			1						x	
Pagurus (unidentified).....				1		2		1		
Antolytus varius Tread.....				3						
Anoplarchus atropurpureus Kitt.....				2	1	5	1	4	1	5
*Cancer oregonensis Rath.....				8	0	6	1	7	1	8
Margarites pupillus Gld.....				12		6	2			4
Gephyrea (unidentified).....					3			1		
*Amphissa columbiana Dall.....					8			3		
Petrolisthes eriomereus Stim.....					6		4	21		
Lophopanopeus bellus Rath.....							9		5	
Acmaea scutum Esch.....						2				2
Hemigrapsus oregonensis Rath.....							1			
Chorilia longipes Dana.....							2			
Polynoe gigas John.....							5		6	
Lacuna unifasciata Carp.....							3	11		
Pentidotea rotundata Rich.....									1	
Epialtus productus Rand.....										4
Ophiurids (3 new species).....		1		16	5			1	1	

*Animals present first uncounted.

Studying the chart using current as an influencing factor we find that: (a) the worms are most generally distributed throughout the beds. (b) The crabs are found in moderate or slow current. (c) The brittle stars are found in the deep swift current. (d) The amphipods are in the moderate and slow water. (e) The snails are most abundant in the moderate or slow current. (f-1) *Epialtus productus* is found only in slow, shallow water. (f-2) Turn Island, probably swiftest current of all places studied had no crabs at all, and Shaw's Island shows similar results. (g) *Lacuna* is most common on leaves; *Margarites* occurs only in holdfasts.

Two factors arise in considering this study: (1) *Nereocystis luetkeana* is an annual plant. Can the holdfast then be considered a permanent habitat? If so, where do these holdfast forms go during the period when the kelps are inactive in late winter? (2) Since so many species studied are the young forms, can the holdfast be considered important for these forms?

Rigg states "many individuals do undoubtedly live through the winter, but the larger number of them in Puget Sound region disappear before they are a full 12 months old." Hurd says that "young plants although not found at all during the winter are quite common in March and April." Setchell says "the active existence is about nine or ten months and within the period of one year." They appear in February and March and disappear about December or January.

From the above, the period of inactivity of the kelp would be three to six weeks at the greatest. Decay of the holdfast would be slow beneath the water, so perhaps taking this into consideration, the old holdfast would serve as a habitat until the young plant of the next season would be large enough for them to take up their abode in it.

Concerning the second point, the adults found in the holdfast are worms, brittle stars and amphipods. These forms are common in large numbers in all beds studied. The other forms, i.e., crabs, sea urchins, etc., are only residents during their young stages.

Rock Bottom Fauna of a Restricted Area near Friday Harbor, Washington*

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and

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During the summer of 1924, under the direction of Dr. V. E. Shelford, an intensive survey was made of the fauna of a restricted area in the San Juan Channel of Puget Sound. The area under consideration was located south and east of Point Caution†. The purpose of the study was to determine the animal communities on the bottom in this region. Representatives of the fauna were secured by means of dredgings at various depths. We are indebted to Professor Trevor Kincaid for the identification of many of the forms.

The area studied was approximately 125 meters long and extended into the channel about 300 meters. The width of the area was determined by a measured line run out from points on the shore. Two points on the shore were chosen which established the limits of the area. The bottom was chiefly solid rock, however, large loose rocks were occasionally brought up in the dredge. A 25 lb. "Bull-dog Snapper" was used to determine the character of the bottom. The line to which the snapper was attached, being marked off in meters, permitted soundings to be made at the same time. The currents in the channel were very strong due to the movements of the tide.

The frame of the dredge was two meters wide and one-half meter high. To this was attached a bag made from one inch mesh web. Beneath the bag and attached to the frame was a piece of canvas of the same size as the bag, which prevented the bag from being torn by the jagged rocks and barnacles on the bottom. The dredge was hoisted to the surface by a gasoline engine. After each haul a record was made of the animals taken. The results are shown in table 1.

*Contribution from the Puget Sound Biological Station and from the Zoological Laboratories of the University of Illinois No. 268.

†See Fig. 1 in Shelford & Towler, animal communities. Publ. Puget Sound Biol. Sta. 5:33-73, 1925.

TABLE 1. Showing the distribution of animals.

Scientific Name	Common Name	47 hauls 26-66M Mean per haul*	32 hauls 67-129M Mean per haul*	Maximum Abund- ance
<i>Pycnopodia helianthoides</i> Stim.....	Starfish.....	0.04		28-44
<i>Cryptochiton stelleri</i> Mid.....	Cryptochiton.....	0.04		26-66
<i>Melibe leonina</i>	Nudibranch.....	0.06		28-44
<i>Pugettia gracilis</i> Dana.....	Kelp crab.....	0.12		26-35
<i>Orthasterias columbiana</i> Ver.....	Starfish.....	0.10	0.03	28-44
<i>Hyas lyraus</i> Dana.....	Lyre crab.....	0.08	0.06	26-35
<i>Ramphocottus richardsoni</i> Gunther...	Grunt fish.....	0.38	0.09	28-44
<i>Stichopus californicus</i> Clark.....	Sea cucumber.....	1.44	0.09	26-66
<i>Strongylocentrotus franciscanus</i> Ag...	Red sea urchin.....	2.14	0.25	26-35
<i>Oregonia gracilis</i> Dana.....	Decorator crab.....	6.23	3.56	28-66
<i>Crossaster papposus</i> L.....	Rose star.....	0.19	0.09	37-43
Unidentified.....	Brittle star.....	0.61	0.62	47-66
<i>Argobuccinum oregonensis</i> Red.....	Large hairy snail.....	2.63	0.37	47-66
<i>Amphissa columbiana</i> Dall.....	Snail.....		0.09	67-87
<i>Nautichthys oculo fasciatus</i> Girard....	Sailor-fish.....		0.09	67-87
<i>Cucumaria chronhjelmii</i> Theel.....	Sea cucumber.....		0.12	67-87
<i>Cancer oregonensis</i> Dana.....	Crab.....	0.23	0.34	67-87
Unidentified.....	Glass sponge.....	0.10	0.62	57-87
Unidentified.....	Stag-horn sponge.....	0.12	0.81	67-87
<i>Calliostoma annulatum</i> Mar.....	Striped snail.....	1.29	1.87	67-87
<i>Pandalus danae</i> Stimp.....	Coon striped shrimp.....	3.31	5.84	67-87
Barnacles (3 species).....	Barnacles.....	4.10	6.81	67-87
<i>Islandis borealis</i> Gilbert.....	Northern sculpin.....	0.02	0.30	67-129
<i>Strongylocentrotus drobachensis</i> Ag...	Green sea urchin.....	0.95	3.65	67-129
<i>Psolus chitonoides</i> Clark.....	Sessile cucumber.....	0.87	5.40	67-129
Brachiopods (3 species).....	Brachiopod.....	6.34	34.03	67-129
<i>Pteraster tessellatus</i> Ives.....	Cushion star.....	0.12	0.18	88-129
<i>Henricia leviuscula</i> Ver.....	Coral star.....	0.14	0.34	88-129
<i>Gorgonocephalus eucnemis</i> Mnt.....	Basket star.....	0.14	0.43	88-129
<i>Pecten hindsi</i> Carp.....	Pecten (rough).....	3.91	4.43	37-43
				88-129

*The means shown in this table were obtained by dividing the total number of individuals collected, by the total number of hauls made at the depths indicated.

The following occasional forms were found in the area: (a) The snails *Trichotropis cancellata* Hinds, *Calliostoma costatum* Martyn, *Margarites pupilla* Gould, *Purpura foliata* Martyn, *Lacuna vincta*, *Calliostoma variegatum* Carp., *Polinices lewisii* Gould, *Neptunea multi-costata* Esch. (b) The mussels *Modiolus modiolus* L., *Lycimerus sub-obsoleta*. (c) Other molluscs were *Calyptraea mamillaris*, *Crepidula adunca* Sow., *Crepidula nivea* (slipper-shell), *Monia macroschisma* Desh., *Pecten hericius* Gld., *Puncturella cucullata* Gould (limpet), Small brown chiton. (d) Other forms were brown rough tunicate, white sea-anemones, *Crego munita* (grey shrimp), octopus, *Hypsagonus quadricornis* Cuv. & Val. (four-horned sea poacher).

The animals shown in the preceding chart form an association in which *Strongylocentrotus drobachiensis* and *Argobuccinum oregonensis* are conspicuous dominants. Therefore it is designated as the Strongylocentrotus-Argobuccinum formation. *Pecten hindsii* and *Oregonia gracilis* were found to be dominants in this area also. Within this formation there were two definite groups, one found in the shallower waters, the other at greater depths. The former has for its most abundant local dominant, *Strongylocentrotus franciscanus*, while the local dominant for the latter was *Psolus chitonoides*. These two groups are called associations and are characterized by these species. Thus, within the Strongylocentrotus-drobachiensis formation there are two associations.

Animal Communities of the San Juan Channel and Adjacent Areas*

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and

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INTRODUCTION

This paper is concerned with a preliminary designation of the animal communities in the area most frequently visited by classes and investigators at Puget Sound Biological Station. No attempt is made to list all the animals in any area. The attention has been focused primarily upon dominant† species in so far as they could be determined.

*Contribution from the Puget Sound Biological Station and from the Zoological Laboratories of the University of Illinois No. 269.

†A dominant species is one which through abundance, size or interaction with other organisms, controls or materially modifies the environment so as to determine what other organisms may occur.

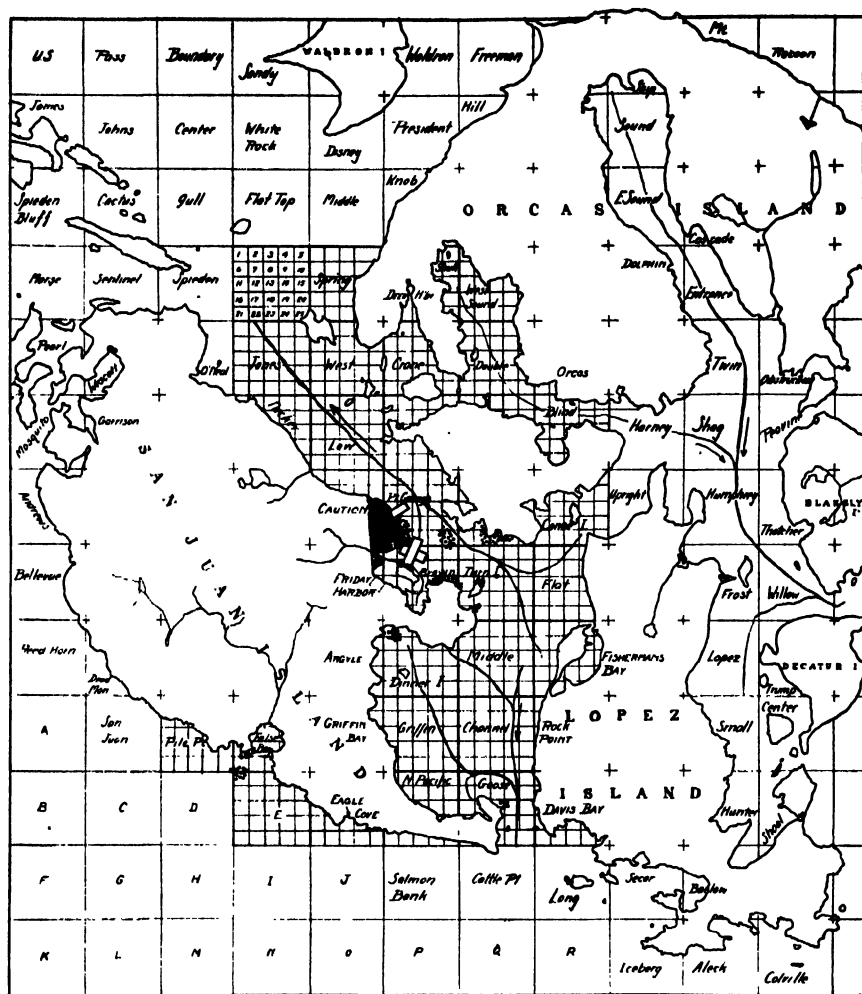


Figure 1. The San Juan Islands adjacent to the Puget Sound Biological Station. The outlines of the islands are shown and in mid-channel the dark heavy lines accompanied by arrows follow the sloping floor of mid-channel into deeper water. The entire region is divided into squares beginning on $123^{\circ} 1'$ west and $48^{\circ} 30'$ north. The large squares are approximately 2780×2780 meters or $1\frac{1}{2}$ nautical miles square and the smaller squares 556×556 meters. The larger squares are named after appropriate natural features. The purpose of the large and small squares is to provide a basis for a complete survey of the region. Special attention has been limited to twelve large squares adjacent to the Biological Station, to two adjacent to False Bay and to two adjacent to Davis Bay and Cattle Point (See Pile Point, False Bay, and Goose-Davis Bay). The oblong areas near the station site indicate the areas of intensive study by Perry, Kirsop, and Essex and Steggerda. The small circles indicate the kelp studies by Andrews.

and upon obvious physical and chemical conditions in the areas covered. The limits of areas have been drawn on the basis of biological rather than physical and chemical phenomena. The importance of such conditions is however recognized. The water within the areas studied reaches a depth of 160 meters. The data which are used as a basis for determining the communities given were gathered principally during the summer of 1922 by the authors, although both have more or less complete records from previous years, the senior author since 1914. He also rechecked the entire field in 1924.

The writers are indebted to Mrs. Ida S. Oldroyd, Professor Trevor Kincaid, and various students and visitors at the Station for identifications and assistance of various kinds.

The general plan divides the San Juan Archipelago into large areas, 1.5 nautical miles or 2780 meters square (see Fig. 1); the small areas are 556 meters square. The starting point for the squares is at $123^{\circ} 1' \text{ W. Long.}$ and $48^{\circ} 30' \text{ N. Lat.}$ The area especially considered covers 12 squares with its center approximately on the shore of the mainland opposite the center of Turn Island. This covers the area immediately adjacent to the station. Four other squares which are not adjacent to the central twelve are included. Of these, two cover False Bay, and two others Cattle Point and Davis Bay (Fig. 4).

GENERAL CONDITIONS

1. Bottom

The general configuration of this Puget Sound area is considered by Mr. Roy D. McLellan to indicate a submerged topography produced by faulting and by glaciation, wave erosion, and deposition (Fig. 1). Figure 3 shows the topography of a part of the bottom of San Juan Channel. There appears to be a ridge between the south end of Fishermans Bay and San Juan Island south of Turn Island. This separates what are apparently two submerged valleys. The one sloping northward receives a branch from north of Flat Point. Another tributary joins the north branch adjacent to the north end of Brown Island. The valley sloping southward from the dividing ridge consists of two branches, one extending nearly due south in mid-channel and the other, rising in North Bay, extending south with the shore of San Juan Island (See Figs. 1, 2, 3 and 4). These valleys appear to have been dammed by terminal moraines southwest of Cattle Point.

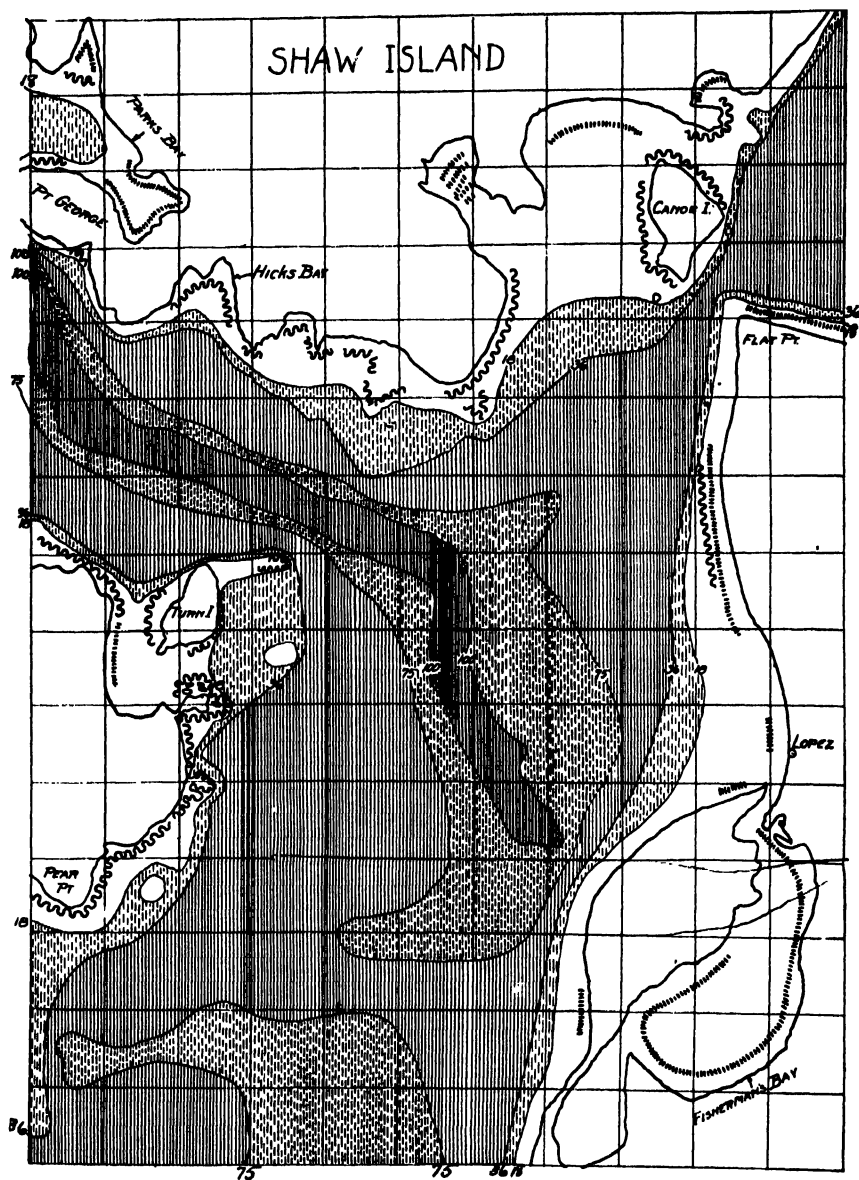


Figure 3. Depth belts, depths in meters, and the distribution of kelp and eelgrass in the center of San Juan Channel, just southeast of the Station. Flat Point, Fishermans Bay, Turn and Canoe Islands and vicinity are important collecting grounds and areas for ecological study. Large squares named Shaw Id., Canoe Id., Turn Id., Flat, Middle and Fishermans Bay in Fig. 1 are covered.

These submerged valleys are U shaped. The sides are often steep. Bottom materials were originally bare rock, glacial till including boulders, sticky clay, sand and gravel. These have been sorted by waves and currents since the retreat of the ice, especially in shallow water. Sticky clay, mud and sand are very local as a rule, the first is in deep water. At the present time the bottom is chiefly rock and other types which include materials for attachment of sessile animals. This is especially true off Point Caution, Georges Point and Cattle Point.

2. Currents

The maximum tidal currents through San Juan Channel probably reach a speed of 8 knots per hour at Cattle Point; four knots is a common maximum throughout wider places. The currents apparently sweep the bottom clean in their main courses. There is often a strong current past Flat Point. Currents set in and out around both ends of Brown Island, Turn Island and Canoe Island, but they are largely confined to the surface. Those about Turn Island are swiftest and deepest. The outer rock on the east side of Turn Island and the eastern exposures of the main land are swept clean. The tide flows into and out of Fishermans Bay providing good circulation, but except in the narrow entrance, it makes only weak currents.

3. Wave Action

Waves in the summer months do not play an important role except outside in Haro Strait and the Strait of Juan de Fuca. Here they are almost continuous and have important effects on the communities of the upper levels.

4. Temperature and Density

The temperature of the open water averages about 11.5°C during the summer months. The lowest temperature recorded in July by Powers is 9.6°C at the surface of the open water; the highest 19°C in a small lagoon. Temperature is usually lower in deeper water in summer.

TABLE 1. *Monthly temperatures observed at Anacortes by H. J. Belch, U. S. Coast and Geodetic Survey.**

	Temperature C			Density reduced to 15° C		
	Max.	Min.	Mean	Max.	Min.	Mean
1921						
Dec.....	8.5	5.5	7.21	1.0220	1.0189	1.02129
1922						
Jan.....	7.0	5.5	6.21	1.0232	1.0216	1.02201
Feb.....	6.5	5.5	6.04	1.0222	1.0218	1.02200
Mar.....	7.0	6.0	6.56	1.0228	1.0218	1.02220
Apr.....	8.5	7.5	7.72	1.0230	1.0219	1.02240
May.....	10.5	8.0	8.89	1.0240	1.0220	1.02277
June.....	15.0	9.5	10.88	1.0227	1.02214
July.....	14.5	10.5	11.80	1.0232	1.0196	1.02170
Aug.....	14.0	10.0	11.61	1.0239	1.0210	1.02230
Sept.....	14.0	10.5	11.50	1.0229	1.0192	1.02200
Oct.....	11.0	9.0	10.39	1.0232	1.0215	1.02239
Nov.....	9.5	8.0	8.97	1.0230	1.0218	1.02232

*Records by the courtesy of the director, Colonel E. Lester Jones, and Professor J. N. Cobb.

5. Osmotic Pressure

The osmotic pressure of sea water having salinity of 35 grams per liter is 22.84 atmospheres. The depression of the the freezing point is 1.9°C. The outlet of San Francisco Bay ranges from 16.6 to 21.64 atmospheres. Similar conditions may be expected in Puget Sound waters. The average during the summer months according to Hurd (1919) at Friday Harbor is 19.204 atmospheres. It varies from hour to hour.

TABLE 2. *Determinations of the depression of the freezing points (Personal communications from Hurd).*

Date (1918)	Hour (P.M.)	Depression	Osmotic Pressure
June 30.....	3:30	1.611	19.37
July 4.....	4:30	1.551	18.65
July 4.....	5:00	1.529	18.38
July 4.....	5:20	1.590	19.12
July 25.....	1.625	19.54

6. Density and Salinity (see table 1)

Density at 0° of sea water with 25 grams of salt per 1000 is 1.02813. The Pacific Coast surface water off San Diego (Michael

1915) is usually about 1.02710 and the salinity approximately 33.70; at 1200 meters, 1.02770 and 34.50. No accurate measurements of Puget Sound water have been made.

Readings by Prof. Kincaid with a 16.5°C hydrometer in the Harbor in front of the Station between June 21 and July 10, 1922 ranged between 1.02028 and 1.02504 (4°/0°). These densities were corrected by the use of Knudsen's tables. According to the tables, these values correspond to salinities of 26.49 (Cl. 14.66) and 32.79 (Cl. 18.15), respectively.

Salinities by the Chlorine Method (AgNO_3) average about 16.9 grams of chlorine. This figure multiplied by 1.8050+.03 gives the total salt in grams per liter. The water about Friday Harbor averages about 0.46 normal chlorine. In the measurement of the H-ion concentration the normality of sea water in chlorine is often desired in connection with making buffers in NaCl solution which corrects the "salt error"; i.e., the incorrect reading of indicators is due to salt. The salt error for 0.50 normal sea water is 0.2 to 0.3 on the Sorensen scale. The indicators read numerically too high or too low in H-ion concentration.

7. Oxygen

The oxygen saturation of ideal (35 gram) sea water at 10°C is 6.5 cc per liter. Fresh water at the same temperature dissolves 8.0 cc per liter. The oxygen content of the open water about Friday Harbor averages about 4.5 cc per liter during the summer months, while pure sea water with 30 grams of salt per liter should dissolve approximately 6.2 cc of O_2 per liter (Jacobsen, 1921). This deficiency suggests a large oxygen consumption by the organisms in the water. Powers found that occasionally the deeper water fell to 3.0 cc per liter. The water is accordingly seen to be deficient in oxygen by from 2.0 to 3.5 cc per liter.

The maximum oxygen content noted by Powers was 12.13 cc among *Ulva* at a depth of 30 cm. The oxygen content at night falls lower among the vegetation than in the open water. Oxygen is nearly exhausted at times in the soil waters of clam beds and like areas.

8. Alkalinity or Alkaline Reserve

Alkalinity or alkaline reserve usually is about 105 parts per million when calculated as CaCO_3 . It is higher in the stagnant water of clam beds. This is a little more than N/500 alkali. The determinations are made by titrating water of pH 8.0 with standard acid. The

alkaline reserve of McClendon (1917) expressed in cc of N/10 acid used per liter is roughly 21.0 on the average (Labbé, 1923).

9. Carbon Dioxide

The waters generally contain free CO_2 . The average amount (with pH 7.8) is approximately 0.75 cc per liter. It ranges from -2 to +2 cc (Birge and Juday). Water bathed with vegetation usually contains no free CO_2 during the day. The total free and combined CO_2 ranges from 46 to 48 cc per liter.

10. Hydrogen Ion Concentration

Expressed in the Sorensen pH figures it ranges in open water from 8.0 to 7.7, in water bathing vegetation 9.3 to 7.7; and in water from clam beds 7.7 to 6.5. The open water is usually 7.9 to 7.8.

11. Iodine Absorption

When all water in which marine animals live is considered it is desirable to determine H_2S and SO_2 . The simplest method of quickly determining these is by titration with iodine, care being taken to prevent losses of the gas into the air either by manipulation precautions or by adding the sample to a known amount of iodine and titrating back with sodium thio-sulphate. N/1000 iodine may ordinarily be used and the absorption calculated as H_2S in cc per liter. Obviously many things besides sulphur compounds will absorb iodine. Plankton, and dissolved and suspended organic matter must be considered as affecting the titration. The results are, however, consistent with depth, circulation, obvious amount of decomposition, etc. The following determinations are representative:—San Juan Channel, 0.10 cc at depth of 1 meter; 0.17 cc at depth of 95 meters; 0.22 cc at a depth of 125 meters; (eel grass) off Flat Point 0.52 cc; Argyle inner lagoon 0.53 cc; Eupogobia holes 0.25-2.00 cc; surface water on clam beds at low tide 0.13-0.77 cc; soil water of clam beds at low tide 0.25-0.75 cc (determinations by Jeffre A. Cunningham).

12. Light

In determining light conditions in Puget Sound waters, five principal things must be kept in mind: (a). Amount of cloudiness; (b). Amount of wind, which both disturbs the surface thus hindering light penetration, and increases the amount of sediment; (c). The flood period for the streams entering the Sound; (d). The sun's zenith distance; (e). The presence or absence of forest fires.

TABLE 3. *Seasonal light relations and factors affecting the same for Puget Sound waters.*

1	2	3	4	5a	5b	6a	6b	7
Mo.	Rain-fall, inches, at Olga	Wind, mi. per hr., Seattle	Flow, ft. per sec., Skagit	Hours Sun-shine	% of possible	Sun's Zenith Distance noon 21st M. col. 1	Hour, with cor. Z. Dist. on June 21	Relative intensity in foot candles*
Jan.	3.2	7.8	3,590	9.0	23	68.4	5:15 P.M.	6058
Feb.	3.1	7.7	1,270	10.5	39	59.0	4:30 P.M.	7391
Mar.	2.5	7.7	2,800	12.1	46	48.7	3:20 P.M.	8306
Apr.	2.4	7.2	5,350	14.0	50	36.5	2:00 P.M.	8979
May	2.1	6.8	9,180	15.5	49	28.3	1:00 P.M.	9246
June	1.5	6.7	8,490	16.0	52	25.5	Noon	9335
July	0.6	5.9	6,010	15.5	62	28.0	1:00 P.M.	9246
Aug.	0.7	5.3	3,200	14.0	57	36.4	2:00 P.M.	8979
Sept.	1.9	5.8	1,960	12.1	48	48.0	3:20 P.M.	8369
Oct.	2.5	6.1	wanting	10.5	35	59.2	4:30 P.M.	7391
Nov.	5.3	7.8	wanting	9.0	16	68.5	5:15 P.M.	6058
Dec.	4.9	7.6	1,830	8.3	18	72.0	6:15 P.M.	5410

*Based on wave length 500 $\mu\mu$.

COMMUNITIES

The controversy as to whether aggregations of organisms or habitats, i.e., the obvious conditions, should be used as a basis for communities is an outgrowth of a lack of knowledge of communities. In papers published in 1911-13, due to difficulties in determining dominant species, the senior writer used physiological criteria for determining communities. While this may be the ultimate aim of ecological study, it is not in general a practical field method. In the twelve years which have since elapsed, little or no progress in the direction of physiological classification has been published. Meanwhile the senior writer's experiments and field experience have led definitely to the conclusion that the distribution and abundance of animals is the best index of conditions obtainable. About the time of the publication of papers based upon the physiological characters in communities, Petersen (1913, published in 1914) discussed the animal communities of the sea bottom exclusive of the fishes and motile species. Fishes were discussed separately by H. Blegvad (1916). There is much information in these papers bearing on the question of dominants and symbiosis, but little of it is in organized form. The lack of recognition of any different grades of communities and

of the relation of the bottom community to the pelagic community above leaves something to be desired.

During the period here referred to, various plant ecologists, notably Clements, have developed the science of plant communities along lines highly practical from the standpoint of field study. The principles find best expression in *Plant Indicators* (Clements, 1920). He recognizes dominants which control the habitat. This practice is similar to that of Petersen who uses those which constitute the bulk of the weight of animal life. Petersen rejects all seasonal animals and, though Clements in a few cases considers them as sub-dominants, up to this point there is agreement. Both would state that the motile organisms should be included but neither has considered them as an integral part of the community. Petersen has built up no nomenclature, while Clements has carried it as far as any justification could be found. The present paper is an attempt to arrange the marine communities along lines based on aggregations rather than habitats.

While there are physiological differences with depth even within the dominants, they no doubt represent the extent of acclimation within the species. As compared with the large differences between animals of the *Balanus-Littorina* formation and the green sea urchin-*Argobuccinum* formation, these differences are very slight (see Shelford, 1916).

After ten years intensive experimental work the writer arrives at the conclusion that in view of the complicated conditions found in relations to environment, a thorough knowledge of communities is essential to thorough experimental analysis.

The names of the communities here used are purely provisional. A study of the same communities over a considerable range, is necessary to show the most general dominants. It is these general dominants, particularly the wide ranging ones, that should be used to name the communities.

The areas near the east of San Juan Island present three communities of the first order. They are dominated by species which occur elsewhere only occasionally. They answer the requirements for the larger land communities called formations. No area on land or in the sea has so characteristic a set of climatic and hydrographic conditions as the intertidal belt, especially on rock shores. The sandy-muddy shores are less strikingly so, though they still retain these characteristics.

1. *Balanus-Littorina* Formation

a. Dominants.

Balanus curiosus Pal. (shore barnacle)

Littorina scutulata Gld. (snail)

Hemigrapsus nudus Dana (purple shore crab)

Acmaea digitalis Esch. (limpet)

Acmaea sp. (limpet)

b. Subdominants.

Littorina sitchana Phil. (snail)

Thais canaliculatus Duclos (snail)

Thais lamellosa Gmelin (snail)

Mytilus edulis L. (mussel)

**Mytilus californianus* Con. (ribbed mussel)

c. Secondary species. *Mitella polymerus* Sow. (gooseneck barnacle); *Diadora aspera* Esch. (keyhole limpet); Serpulids; Idotea (*Fucus* isopod), etc.; Echinoderms which invade especially from below are *Pisaster ochraceus* (Br.) Ag., *Strongylocentrotus drobachiensis* Mul., etc.; green and red sea anemones; under rocks at the lower edge occur *Xiphidion mucosum* Gr. and *Anoplarchus atropurpureus* Kitt. (both blennies).

d. Influence of substratum. This formation is usually found upon a hard substratum, such as rocks, wood, boulders or gravel, between the tide lines. Water movement in the form of tidal currents influences the size, the abundance of dominants and subdominants, and the presence of secondary species of all kinds including those which are dominant lower down but at times occur at considerable height above low tide.

Wave and tide action. From table 5 and figure 8 the general luxuriance of the communities can be seen. These differences appear to be correlated with the amount of wave and tide action against the shore. The length of the periods of exposure and of submergence is of great importance as a rule, but Huntsman (1918) found that high temperature and reduced salinity may take the place of exposure to air. His observations were made at Cheticamp, Cape Breton Island. Here the relations to the lower communities remained the same as on the Atlantic Coast, but the intertidal species extend down into the low salinity water 20 meters or more.

Height of tide. The zero of the tide book is approximately 0.8 meters below the mean of all low tides. The mean of all low tides is approximately the upper limit of Ulvaceae and of the animals

*A dominant in some localities (Edmondson, 1920).

which live chiefly in the water at deeper levels. The mean of the highest of the two tides corresponds approximately to the highest level occupied by animals occurring on shore.

Length of exposure and of submergence. That the length of time of exposure by the falling of the tide has much to do with the variation noted in animals of the same species between lower and higher intertidal levels is common knowledge to all investigators. No animal getting its food from the plankton carried to it in the sea water can exist without a fresh supply of food. Barnacles, for example, must often live many hours exposed to a hot sun and subject to dessication as well as extreme ranges of temperature. This seems to be essential to the existence of some species since they begin feeding as soon as they are submerged.

The following table was prepared by estimating the average time that each level was submerged according to the data given in the tide tables published by the U. S. Coast and Geodetic Survey. By graphing the tides and comparing the time of submergence with the estimated time given by the tide tables it was found that the graphs were approximately accurate.

TABLE 4. *Time of exposure and of submergence in hours and per cent for four months of 1922. (E.D.T.)*

	Jan. 733 Hrs.		June 720 Hrs.		July 737 Hrs.		Aug. 744 Hrs.	
	Cov.	Ex.	Cov.	Ex.	Cov.	Ex.	Cov.	Ex.
- ½ meter.....	733	0	718	2	737	0	744	0
Per cent.....	100	0	99.72	.28	100	0	100	0
0 meter.....	724	9	696	24	705	32	735	9
Per cent.....	98.77	1.23	96.66	3.34	95.66	4.34	98.79	1.21
½ meter.....	696	37	642	78	671	66	690	54
Per cent.....	94.95	5.05	89.17	10.85	91.05	8.95	92.74	7.26
1 meter.....	615	118	570	150	582	155	595	149
Per cent.....	83.91	16.09	79.17	20.83	78.97	21.03	79.97	20.03
1½ meters.....	502	321	437	283	444	293	453	291
Per cent.....	68.48	31.52	60.69	39.31	60.24	39.76	60.88	39.12
2 meters.....	316	417	231	489	254	483	224	520
Per cent.....	43.12	56.88	32.08	67.92	33.21	66.79	30.11	69.89
2½ meters.....	93	640	56	664	52	685	24	720
Per cent.....	12.67	87.33	7.77	92.23	7.03	92.97	3.23	96.77
3 meters.....	6	727	0	720	0	737	0	744
Per cent.....	.82	99.18	0	100	0	100	0	100

Moisture and shade. These are essential for an abundance of gasteropods. Thais is usually low down in this belt but goes nearly to high tide in cracks and along the edges of tide pools. Littorina is less abundant on the sunny shores.

Vegetation. Fucus is likely to shelter many Littorinas. Young barnacles are numerous but it appears that they do not develop. Numerous small limpets occur under the Fucus, and has led some observers to the conclusion that it is important as a shelter for the young. An isopod is probably largely confined to the Fucus, in the Puget Sound region.

e. Growth forms. The height to which barnacles and gasteropods go and at which they reach their maximum abundance and maximum size varies with exposure. There are localities in which the height above low tide cannot be made the subject of generalization because of differences of shore topography, though differences in height exist. *Littorina scutulata* is largest on the exposed side of Brown Island while *L. sitchana* is largest on the protected inner side. *Acmaea digitalis* is largest on exposed situations and smallest on less exposed situations, and grows largest on the open shores of the Straits of Juan de Fuca.

Barnacles are subject to variations which result from favorable conditions of seeding followed by crowding, as well as from conditions favorable for growth. Rock reefs near Olga show sets in innumerable quantities and larger barnacles crowded into masses. The individuals are about 5 cm high and in many cases as small as a lead pencil, being crowded together like the cells of a honey comb. Where thinning has taken place, due to some individuals falling off rotten piles, some of the largest tall barnacles occur. Similar tall slender forms of *Balanus balanoides* occur on the Atlantic Coast (Pilsbry 1916). A small local area at Mya Cove, Davis Bay, showed very few sets and large short adult barnacles. The observations suggest that optimum conditions for growth and for seeding are not the same. Where conditions are favorable for both, crowding results in the tall slender forms.

f. Associations. Two associations may be recognized: *Balanus*-(*Mytilus*) *californianus* Association and *Balanus*-(*Mytilus*) *edulis* Association. (1a and 1b, Fig. 5, 6, and 7).

Balanus-californianus association. It occurs on rocks, more or less vertical, jagged and rough, exposed to constant circulation with considerable wave action as in the Straits of Juan de Fuca and more open waters, probably of high salinity, etc. More types of algae

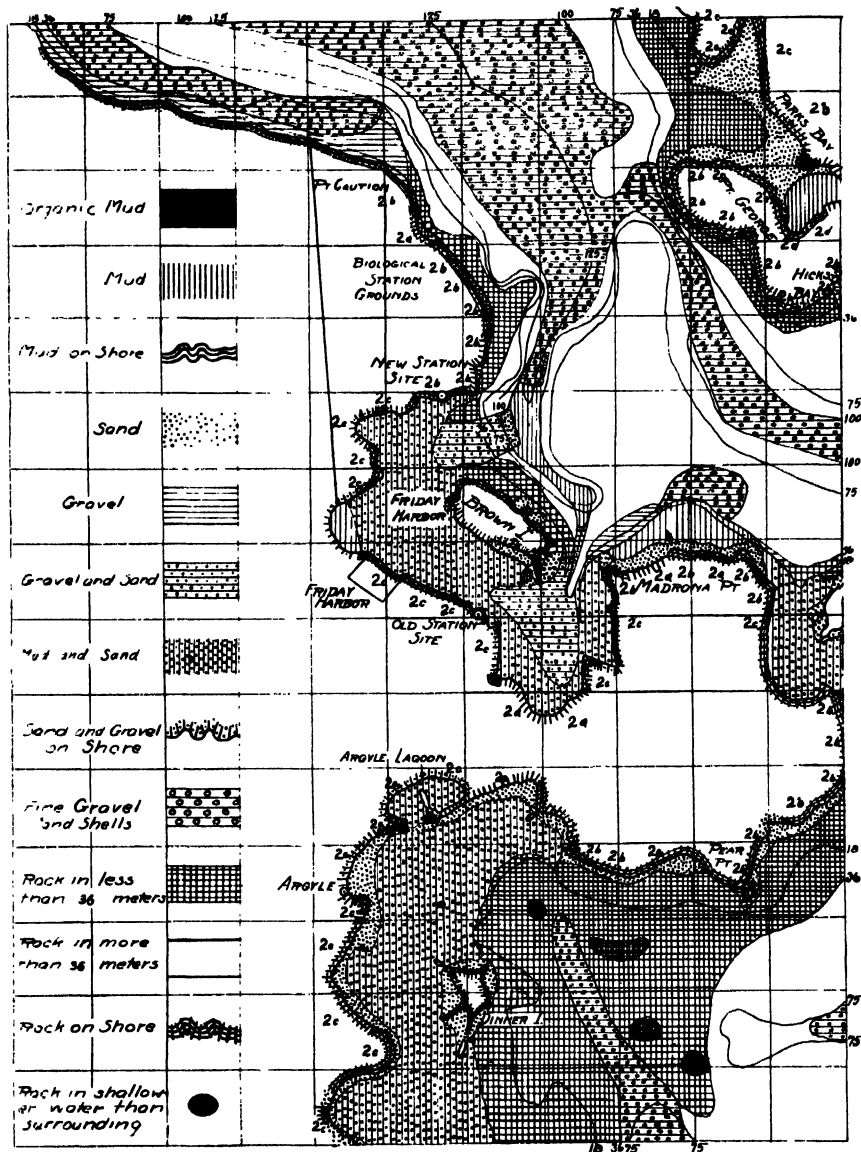
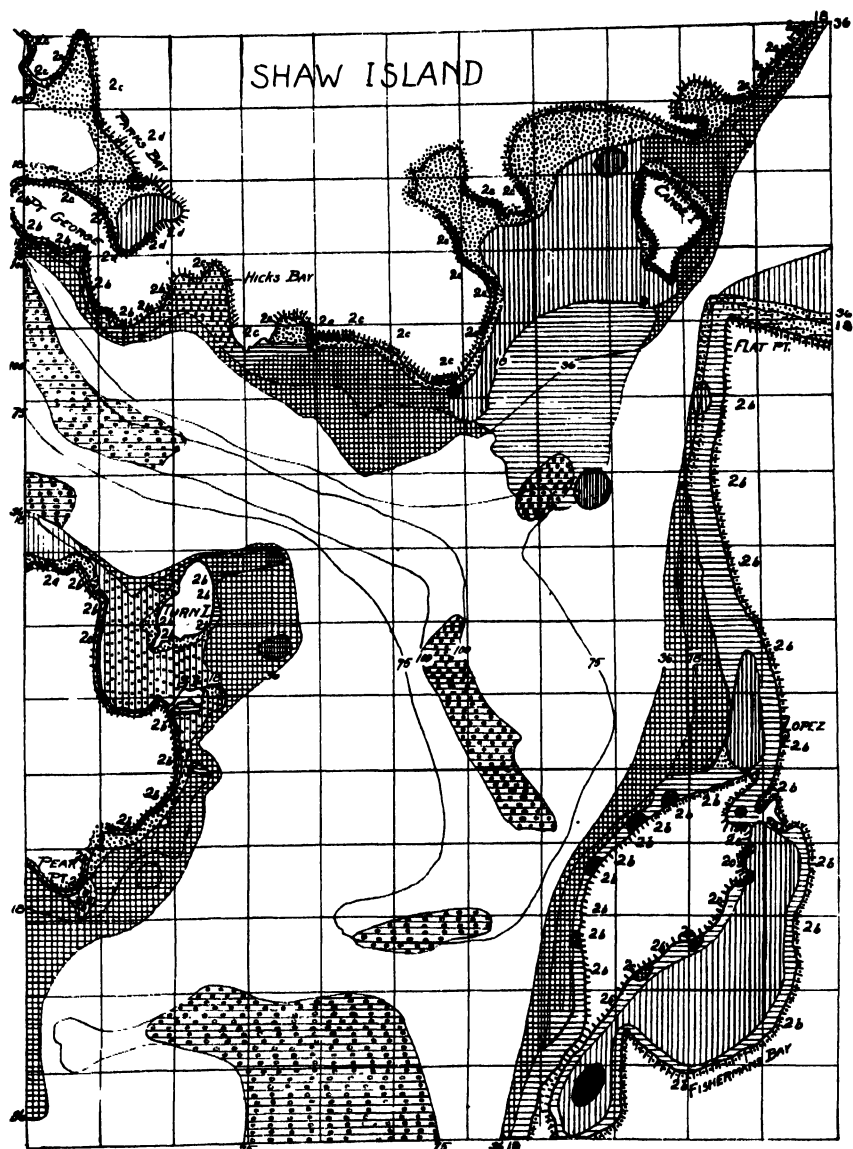


Figure 5. Kind of bottom and distribution of communities. The figures along shore refer to the Balanus-Littorina formation; figure 1a indicates luxuriant Balanus-californianus associations, figure 1b less luxuriant types of the same association (see table 5 and Fig. 8), 2a, 2b and 2c indicate similar degrees of luxuriance of the Balanus-edulis association.

The four communities which make up the Macoma formation, namely, Macoma-Paphia, Macoma-Leptosynapta, Macoma-Eupogebia, and Macoma-Haminoea associates are not indicated here. Mud, sand or other fine bottom materials and the



presence of eelgrass (see fig. 2, 3, and 4) suggest the probable presence of these communities where the depth does not exceed 5 meters.

Below 0 meters on rock or gravelly bottoms and below 5 meters on other bottoms the *Strongylocentrotus-Argobuccinum* formation is practically continuous. The 36 meter line marks roughly its division into associations although under conditions of strong circulation the differences may occur at a greater depth (see Essex and Staggerda). The distribution of communities can be shown only on large scale maps.

Figure 6. Similar to figure 5. Compare with figure 3.

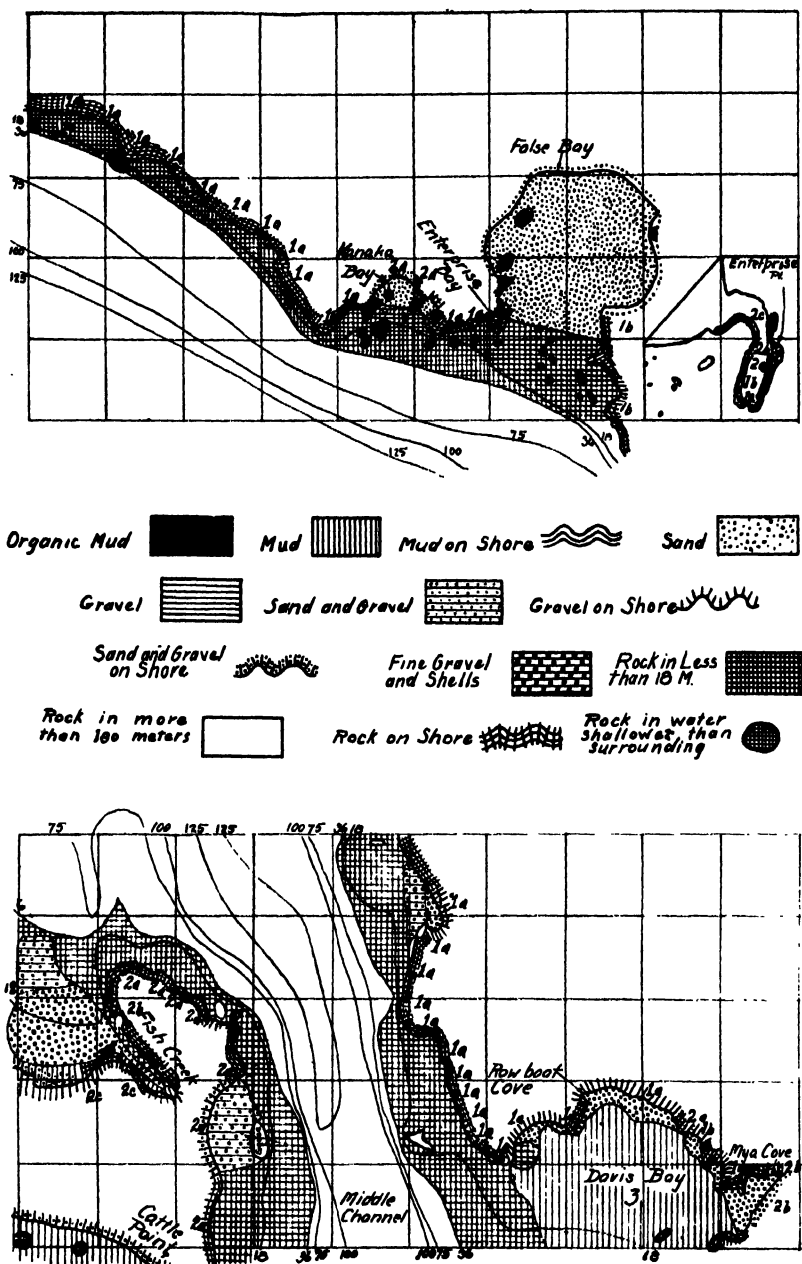


Figure 7. Bottom and communities in the vicinity of False Bay and Davis Bay. Compare with figures 4, 5 and 6.

occur and usually the individuals are larger. The community includes numerous species of large animals. The formations dominant are all present and of large size. Characteristic subdominants are *Mytilus californianus* Con. (ribbed or California mussel); *Diadora aspera* Esch. (keyhole limpet). Red sea-anemones are more frequently present than in the other associations. *Mitella polymerus* Sow. (gooseneck barnacle) forms clans in crevices. Nothing is published as to the relation of fishes in this community at high tide.

Balanus-edulis association. *Mytilus edulis* Linn., the small mussel, is found here as a subdominant equivalent to *M. californianus*. The circulation of water is slower; there is little wave action in the enclosed waters where they occur. Gooseneck barnacles and California mussels are not found here. The other dominants and subdominants are numerous, smaller and irregular in occurrence. The common starfish, *Pisaster ochraceus* (0 meters), is more common here than in *Balanus-californianus* association. In general, the number of individual animals of the same species found in the best *Balanus-edulis* associations may be estimated at from $\frac{1}{4}$ to $\frac{1}{3}$ of those found in the *Balanus-californianus* associations. The communities are still more reduced in enclosed bays, and on boulder beaches. They may be scantily represented on coarse gravel above the *Macoma* communities on some beaches. The communities with crowded barnacles, referred to above, appear to have no characteristic subdominants and are essentially *Balanus-edulis* associations. The occurrence of the *Balanus-edulis* association on the small islands and reefs north of Orcas Island, where tides are strong and wave action severe, indicates that various hydrographic factors besides circulation are important. Their proximity to the Fraser River suggests that salinity and correlated factors are of much importance.

Relations and distribution of the two associations. The piling of wharves is usually occupied by communities of the *Balanus* type. Under certain conditions several degrees of luxuriance of the two associations may be recognized and the transitions from one to the other traced within a few meters. This is true where protected enclosures occur in connection with the more open bodies of water. One of the best examples is to be found along the west shore of False Bay adjacent to Enterprise Cove (Fig. 7). The distribution of the two associations and the various degrees of luxuriance is shown in Figs. 5-8 and in table 5.

Species belonging lower down are exposed at tides lower than the average, and one source of confusion lies in their inclusion with

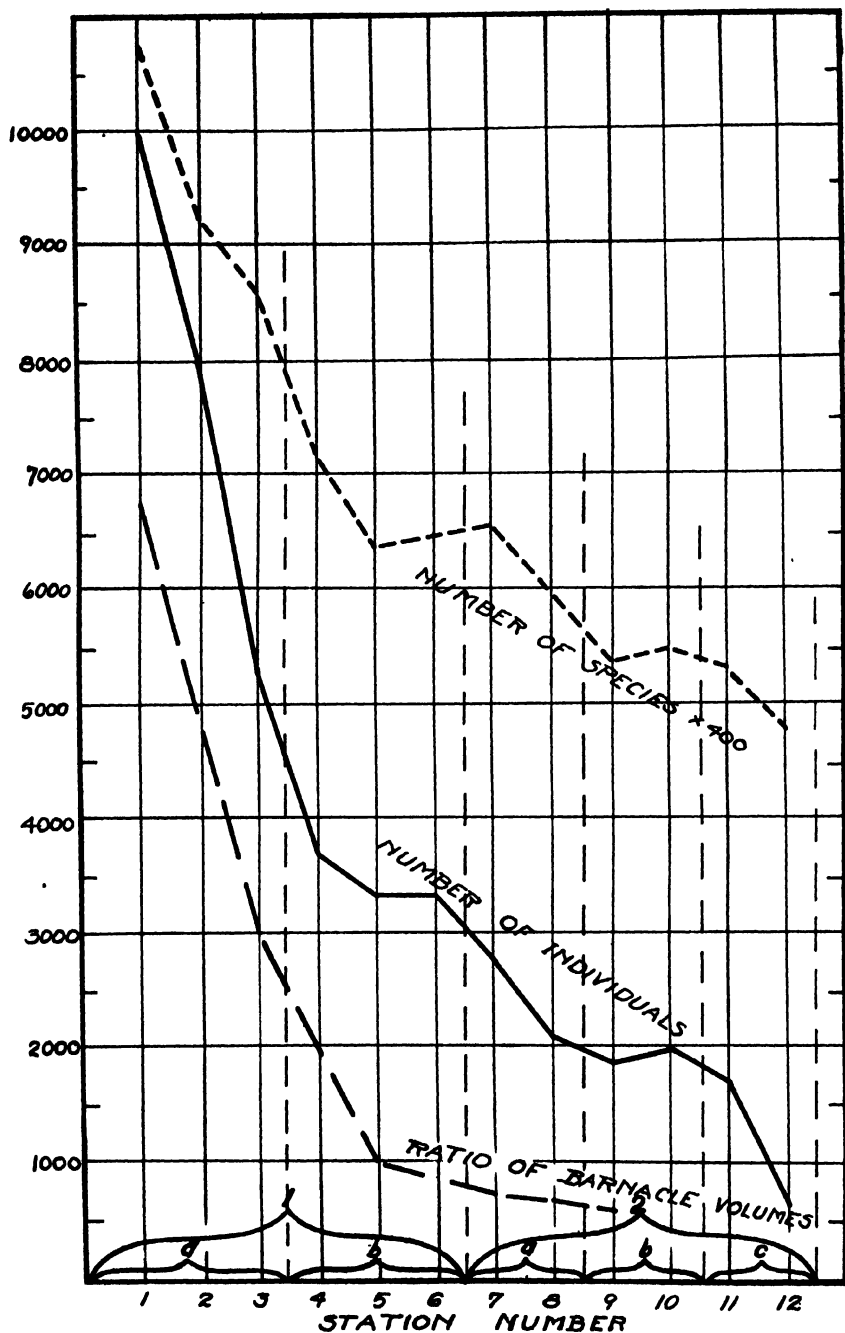


Figure 8. Size of barnacles, number of individual animals of all kinds, and number of animal species along the east side of Enterprise Point. Readings were taken at each of 12 stations. The groupings numbered 1-2 and indicated by parentheses represent the different types of communities, two or three stations representing each.

TABLE 5. *Distribution of animals on the intertidal rocks and subtidal rocks exposed at low tide in False Bay: l, large; m, medium; s, small; n, numerous; c, common; f, few.*

I. *BALANUS-LITTORINA* FORMATION

ASSOCIATION	Balanus-californianus; 1						Balanus-edulis; 2					
	a			b			a		b		c	
STATIONS	1	2	3	4	5	6	7	8	9	10	11	12
<i>Mitella polymerus</i>	lf		lf	lf		lf						
<i>Mytilus californianus</i>	ln	ln	mc	mc	fs	fs						
Serpulid worms.....	mc		mc		mc		mc			mc		
Green anemones.....	ln	ln	ln	lf	ln	ln	lf	ln		lf		
<i>Thais</i> sp?.....	ln	ln	ln	mc	mc	mc	mc	mc	sf	sf		
Isopods.....	ln	ln	ln	ln	ln	ln	ln	ln	lf	lf		
<i>Katherina tunicata</i> Wood..	ln	ln	mc	mc	mc	mc	mf	mf	mf	sf		
<i>Acmaea</i> sp?.....	ln	ln	ln	ln	ln	ln	ln	ln	mn	mn	sf	sf
<i>Acmaea digitalis</i>	ln	ln	ln	ln	ln	ln	mn	mn	mc	mc	sf	sf
<i>Littorina</i> sp?.....	lf	lf	ln	ln	ln	ln	ln	ln	ln	ln	mn	mn
<i>Balanus cariosus</i>	ln	ln	ln	ln	mn	mn	mn	mn	mn	sn	sn	sn
<i>Hemigrapsus nudus</i>	lf	lf	lf	lc	lc	lc	lc	lc	lf	mf	sf	sf
<i>Mytilus edulis</i>			sf		sf		sf		mc	mc	ln	lc

II. *STRONGYLOCENTROTUS-ARGOBUCCINUM* FORMATION

* <i>Calliostoma costatum</i>	lf											
* <i>Caularchus meandrichus</i> ..	lf											
* <i>Pisaster ochraceus</i>	lf	lf										
* <i>Diadora aspera</i>	lf	lf	lf									
* <i>Cucumaria miniata</i>	cf	cf	cf	cf								
* <i>Epilatus productus</i>	lf	lf	lf	lf	lf	lf						
*Red anemone.....	lf	lf	lf	lf	lf	lf	lf					
*Sponge.....	mc	mc	mc	mc	mn	mn	mn					
* <i>Henricia leviuscula</i>	lf		lf		lf		lf					
* <i>Leptasterias aequalis</i>	lc	lc	lc		lc		lf	†	†	†	†	†

*Occasionally above mean low tide.

†Macoma formation below these stations.

the *Balanus* Formation. These are starred in table 5 and make up the greater part of the list. The starred species tolerate short exposures to air and reduced salinities while the others require these.

g. Succession. Little or nothing regarding succession appears in published accounts. Brandt's (1897) account of the populating of the Kiel Canal is one of the outstanding studies. Here succession was rapid, being well on its way toward a climax within two years. There is every indication that succession on rock is very rapid, requiring less time than is indicated by the Kiel Canal studies.

h. History.

In 1848 Sir Edward Forbes recognized the Inter-tidal belt as the Littoral Zone (between the tide lines), and named other zones lower down (see Johnstone).

King & Russel (1909) elaborate a series of zones based upon habitat analyzed in detail with amount of fresh water and sea weed zones emphasized. Their data indicate that certain species (*Littorina*, *Balanus*, etc.) occur throughout the intertidal belt and that associations could be recognized on the basis of other dominants.

Apellöf (in Murray & Hjort, 1912), referring to the Norway coast, does not distinguish the intertidal community as a major community but calls all from the upper limits of marine life, to 30 or 40 meters the "littoral zone." He recognizes an intertidal belt as secondary. This appears however to be very much like our Pacific coast intertidal belt.

Pearse (1913) discussed the rock beaches of Nahant. It appears that *Balanus balanoides*, and *Mytilus edulis* are dominants. He states that the latter occurs in protected situations clear up to the top of the barnacle zone. *Littorina rudis* often occurs above the barnacles. *Purpura lapillus* occurs, but the level which it occupies is not made clear. The account makes evident that the levels at which the species occur are dependent upon exposure. The animals belonging to the subtidal belt are not clearly separated from the regular intertidal inhabitants. This is perhaps due to a failure to recognize mean low tide as opposed to some lower points, though the presence of hydroids on plants which are exposed daily would serve as a character distinguishing this community from those of the Pacific coast.

Hedley (1915) described the intertidal communities about Sydney, Australia, and mentioned three height zones.

Colton (1916) has referred to the *Balanus* (Intertidal-Rock) Formation of the Maine coast as the Littoral Formation. The dominant here is *Thais lapillus*, with *Balanus balanoides* and *Mytilus edulis* as subdominants (part personal communication).

Johnson (1917) working on the coast of Queensland recognized five zones in the intertidal belt, all based upon dominant animals. The upper three correspond to Hedley's upper zone, the other two to his median and lower. From Johnson's description, here again, it appears that on the basis of dominants, two aggregations dominated by different species, or at least two associations, may be recognized as described by Colton (1916). It is not clear that the lowest zone of both Hedley and Johnson is not the upper edge of a sub-tidal belt, as no sub-tidal data were presented.

Flattely and Walton (1922) used the habitat as the basis for the communities corresponding to our *Balanus* community. Stratal societies may be said to be recognized, in that animals are divided into those living on stones and those living under stones. However the distinction between animals requiring exposure or reduced salinity and those tolerating it is not made.

Oliver (1923) has published an excellent account of the communities about New Zealand. His studies cover a much larger area than ours and hence are concerned with greater diversity. His use of "growth form"* as applied to animals is difficult to justify. We have used growth form as applying to differences in size and form occurring as response to environment and such parallel differences as might be found in similar types of animals. Oliver used snail, bivalve, and barnacle types as growth forms. Plant ecologists would hardly refer to the desmid, toadstool, and coniferous tree growth forms. Growth form has been used by them primarily to apply to different forms of the same organism under different conditions and differences of the same magnitude and type in other species. We are not able to accept Oliver's growth form view, but the work of the Australian and New Zealand investigators generally is superior to most European and American work covering rocky shores.

Beauchamp (1923) used the habitat as the primary basis for the classification of communities.

Balanus communities are poorly developed at Woods Hole, and Allee (1923) appears to emphasize the habitat more than the dominants. He does not separate very clearly, the Intertidal Formation from the submerged communities, due no doubt to the small rise and fall of the tide, and small number of rocks.

*Since this article was written the authors' attention has been called to the fact that Oliver has used the term growth form in the sense in which it has been used in Warming's "Plant Ecology" (English Translation). There have been some protests against this (see Clements, 1920:68). Life form might be applied just as Oliver used the term "growth form" and is preferred.

2. *Macoma* Formation

This is a community dominated by clams, worms, etc. As a rule it includes a belt of eelgrass near its lower border. The clams come up within 30 cm of the average high water on fine bottom materials and go about a meter or more below mean low tide. Subdivision of the formation on the basis of dominants is usually possible. Dominants are more important and uniform as a basis for such subdivision than the differences in depth and circulation often associated therewith. It is on bottoms of gravel, sand or mud.

a. *Dominants.*

Macoma nasuta Con. (bent-nosed clam), *M. secta* Con. and *M. inquinata* Desh. (clams)

Paphia staminea Con. (butter clam, or little-neck clam)

Saxidomus giganteus Desh. (giant clam)

Oligocottus maculosus Gir. (tide pool sculpin)

Psettichthys melanostictus Ger. (black-spotted flounder)

Platichthys stellatus Mart. (starry flounder)

Nereis virens Sars. and other clam worms

**Leptosynapta inhaerens* Ver. (footless holothurian)

**Echinarachnius excentricus* Esch. (sand dollar)

**Hypogebia pugettensis* Dana (marine crawfish)

**Arenicola claparedei* Lev. (smooth clam-worm)

Cancer productus Gib. (edible crab)

Cancer magister M-E. (edible crab)

b. *Subdominants.*

Cardium corbis Mart. (cockle)

Schizothaerus nuttallii Con. (Washington clam)

Hemigrapsus oregonensis Dana (hairy shore crab)

Telmessus cheiragonus Rath. (helmet crab)

Sebastes nebulosus Ayres (yellow-spotted rock-fish)

Cymatogaster aggregatus Gib. (viviparous perch)

Pholis ornatus Gir. (green or chameleon blenny)

c. *Secondary species* include hydroids, sea anemones, sessile jellyfish, etc. Crustacea such as *Caprella* are abundant. Some amphoids and occasional shrimps occur on the eelgrass. One or two species of shrimps occur on the surface of the bottom locally.

d. *Influence of conditions.* The effects of waves and currents are greater here than for any other communities studied. Deposition of sand, silt and organic matter is important. The fact that an area is sand is usually evidence that deposition is going on, though

*Restricted in range.

when facing the open ocean or the larger open bays, an area often shows permanent clear sand, and affords a fairly stable habitat. Enclosed and protected areas rapidly accumulate sand, silt and especially organic matter; in most cases they tend to become black muck bottomed swamps, and finally dry land. As this process goes on the bottom fauna is sometimes buried during stormy periods; as a rule there is an accumulation of organic matter, an increase in CO_2 , H_2S and other products of decomposition in the waters which fill the bottom soil in which many animals live. There are greater variations in temperature, hydrogen ion concentration, oxygen, etc. The vegetation usually becomes denser, and dry land finally formed.

e. Growth forms. The clams probably show shell differences in the different stages of the community but these have not been studied. Likewise there may be differences in hydroids, etc., which are uninvestigated.

f. Associations and associes. This formation may be divided into two associations differing primarily in dominants. One is usually in deeper water than the other but no definite rule can be laid down. The bottom materials differ materially particularly with reference to the amount of organic matter and size of particles, but these differences are not well correlated with the animals present. These communities, now existing, are probably sea climax communities on the cleaner bottoms, but those in the more stagnant waters are probably stages in a series of habitats leading to dry land. There are also two subdivisions of the formation roughly correlated with the circulation of the water. These two subdivisions are each roughly divisible into the depth belts noted above. Circulation is more important than depth; a comparison of different beaches shows that distribution is determined by those hydrographic conditions which find rough expression in the term circulation and those conditions correlated with them; depth is a lesser factor. In other words the organisms are indicators of general conditions of which depth is one of the less important.

Macoma-Paphia association. Where circulation is good the area between the mean low and mean high tide lines is not well supplied with animals. There is little or no *Ulva* or other vegetation. *Paphia staminea* Con. (butter clam), *Psephidia lordi* Baird, the introduced *Mya arenaria* L. and Nereid worms are the dominants between mean low and mean high tide.

Macoma-Leptosynapta association. The eelgrass usually present in this belt is more or less local. The footless holothurian (*Leptosyn-*

apta) is usually present with *Macoma* and other wider ranging clams. Sometimes *Arenicola* is fairly abundant. Sand dollars (*Echinarachnius excentricus*) are abundant but very restricted occurring as clans occupying a very narrow depth belt much more restricted than eelgrass or any associated animals. It occurs below the *Macoma*-*Paphia* association.

Macoma-Eupogebia associates.* It is characterized by *Eupogebia* from near high tide to mean low tide. On the upper edge the hairy shore crab takes the place of the shore crab of rocky shores. Worms (*Nereids*, *Amphitrite*, etc.) are common.

Macoma-Haminoea associates. Eelgrass occurs generally on protected sandy shores (1-5 meters below high tide). Many young forms live on the eelgrass until they are able to care for themselves. The pH of the water bathing eelgrass ranges from 8.8 to 7.7. The lowest H-ion concentration was outside Argyle where vegetation was dense and the sun was shining. Highest readings are to be expected here when vegetation is decaying during the winter months. Temperature over eelgrass during the middle of July ranged from 10.2°C at Brown Island to 15.1°C outside of Argyle where highest temperatures are to be expected.

Haminoea breeds here during the summer. It appears to die after breeding. The *Macomas* continue well down into the eelgrass and below. The helmet crab, cancer crabs and yellow spotted rock fish are nearly always present. The viviparous perch is often abundant especially in tide pools. It occurs below the *Macoma-Eupogebia* associates.

g. Succession. This community type shows a phenomenon which we believe has not often been touched upon by ecologists. A marine community which is probably climax develops upon new clean sand. In this case probably the *Macoma-Leptosynapta* association (deeper water) and *Macoma-Paphia* association are the marine climax. If the community is to start changing to a land type, the formation dominants especially *Macoma* remain dominant throughout, even in the late stages toward land. The *Eupogebia* community (bare strand belt) is called an associates and the *Haminoea* or eelgrass (submerged) another associates because of different dominants. Such conditions were discovered in a small pocket adjacent to Fisherman's Bay. *Macoma* remains after *Eupogebia* has dropped out.

The sea climax undergoes a retrograde succession to swamp and finally land conditions. The *Eupogebia* and *Haminoea* associates may

*A subclimax or developmental community of associational rank.

be regarded as representing the early stages of this retrogression. There are perhaps older stages which precede conditions noted at Fishermans Bay (e.g. at Argyle Lagoon) but they have not been studied from this viewpoint as yet.

h. Other localities. The *Macoma* communities of the Danish waters (Petersen 1913, 1914 and 1919) extend deeper as concerns eel-grass, down to 12 m., and in addition there is a lower belt reaching down to more than 30 meters. This does not occur in the Puget Sound areas studied, though there is little doubt but that it is the same formation type. Blegvad (1914 and 1916) gives an excellent account of this type of community in certain Danish localities taking into account the interrelation with particular reference to fish.

Allee's *Phascolosoma* Association appears nearest to this type and differs from European and Pacific communities in apparently being without bivalve dominants, except perhaps *Venus mercenaria*.

Ford's (1923) study of the communities about Plymouth, England follows the excellent example of Petersen. He uses the term association and formation somewhat loosely but the phenomena admirably suited to the use of Clement's nomenclature are indicated.

3. *Strongylocentrotus-Argobuccinum* Formation

This community is very largely subtidal. In the San Juan Channel it extends down to a depth of 150 meters at least. Investigation has been very meagre below this level. The same assemblage of species occurs practically over the entire bottom of the channel. There are areas more luxuriant than others, areas in which certain of the dominant species are more prominent than others but on the whole there is little important difference in the different parts.

a. Species included among the dominants.

Strongylocentrotus drobachensis O. F. Mul. (green sea urchin)

Argobuccinum oregonensis Red. (large snail)

Calliostoma costatum Mar. (snail)

Psolus chitonoides Clark (sessile echinoderm)

Henricia leviuscula Fish. (blood star)

Oregonia gracilis Dana (crab)

Tricopterus cancellatus Hinds (snail)

**Pecten hindsii* Carp. and *P. hericius* (scallop)

**Balanus nublis* Dar., *B. rostratus* Hock., *B. balanus pugettensis* Pil.
(barnacles)

*The distribution of these has not been fully worked out from the standpoint of species but all of the two or three are well distributed over the bottom.

b. Species included among the subdominants.

Strongylocentrotus franciscanus A. Ag. (red sea-urchin, locally dominant, 0-36 m. but subdominant, 36-125 m.)

Modiolus modiolus Lin. (deep water mussel)

Terebratalia transversa Sow. and other species of brachiopods

Crepidula nivea Ad. and other species (slipper shell)

Stichopus californicus Ed. (large cucumber)

c. Secondary species. This list should include the less abundant species and those which occur only locally or seasonally. The hydroids, some bryozoa and nearly all the algae come in this class.

d. Influence of conditions.

Currents. Waves and currents have far less effect than in shallow water. Currents are most important in the narrow channels where they afford conditions for a luxuriant growth of barnacles, hydroids, and hydroids, but the difference is one of abundance rather than a change in dominants.

Bottom. The community is best developed on rock bottom but the shells of mollusca, boulders, or even hard sand in deep still water supports the same types as the harder bottom.

Vegetation. This is of little significance. There is no such thing as a Laminarian belt as algae do not occur over the entire depth belt but only in places. The red algae are still less certain to be present. They die down for a part of the year. Various algologists have given these aggregations of algae associational rank, whereas they would for the most part be considered seasonal societies or at most consociations.

e. Physiological differences. Conditions of the seawater vary at different depths. Temperature is nearly always lower in the deeper water here. The hydrogen ion concentration is usually higher in deeper water. Powers found in the summer of 1920 that the pH is sometimes high at the surface, lower deeper down, and higher again still deeper. Salinity is usually greater in deeper water though the column may at times be inverted, perhaps due to tidal currents.

The physiological differences due to depth are well illustrated by the reactions of animals to fresh water, desiccation, rheotaxis, gradients, etc. Table 6 illustrates this.

TABLE 6. *Physiological differences correlated with depth.**

	Depth M.	Survival Time in Minutes								Order of Orienta- tion†
		Fresh Water			High Temp.		Acid		Alk.	
		1	2	3	1	2	1	2	1	
1	+2		f157	m		f190				
2	0					g17		g117		
3	1							h30		
4.	4	a25	i140		a34	i13	a55		a60	
5.	10		j62		d91				e67	o 2.9‡
6.	15	a23			a27					a 1.8
7.	20					j8	a190		a60+	
8.	30			k315						
9.	40	a13			d5					a 2.5
10.	50			n100	a21		b87			
11.	60	b9								
12.	70	e25			b9 c11					
13.	80				a13					
14.	120	c7			a12½ c8					q 5.8
15.	140	e6								
16.	160				c7		b100		e97+	

*The species involved are indicated by letters as follows: the letters being prefixed to the survival time in minutes for the species in question.
†In decreasing current velocity.

‡The average of the 1st, 2nd, etc., of several species.

- | | |
|---|---|
| a. <i>Pandalus danae</i> Stimp. | j. <i>Pugettia gracilis</i> Dana. |
| b. <i>Spirontocharis lamellicornis</i> Dana | k. <i>Crossaster papposus</i> Lin. |
| c. <i>Pandalus stenolepis</i> Rath. | l. <i>Pteraster tessalatus</i> Ives. |
| d. <i>Crangon alaskensis</i> Lock. | m. <i>Mytilus edulus</i> Lin. |
| e. <i>Paracrangon echinata</i> Dana. | n. <i>Modiolus modiolus</i> Lam. |
| f. <i>Hemigrapsus nudus</i> Dana. | o. <i>Spirontocharis brevirostris</i> Dana. |
| g. <i>Petrolisthes eriomerus</i> Stimp. | p. <i>Pandalus borealis</i> Kroy. |
| h. <i>Cancer productus</i> Rand. | q. <i>Spirontocharis alaskensis</i> . |
| i. <i>Teimessus cheiragonus</i> Tll. | |

f. *Growth forms, etc.* There has been little study of growth forms in this community (Dubois, 1916). There are differences in color of crustacea, especially shrimps. Those from deeper water are usually lighter in color, and the eyes of deep water specimens have a brilliant fiery shine.

g. Associations. Two associations can be recognized and some others suggested.

Strongylocentrotus-Cucumaria miniata association. There is an association in 0-36 or 50 meters depending upon strength of currents which corresponds to Hjort's "Littoral" belt. It includes algae in some places and is characterized by the following subdominants:

Cucumaria miniata (japonica) (red cucumber)

Caularchus meandricus (Gir.) (cling fish)

Pholis ornatus (Gir.) (chameleon blenny)

Bryostemma decoratum J. & S. (decorated blenny)

Petrolisthes eriomereus St. (porcelain crab)

Lophopanopeus bellus St. Roth. (black-clawed crab)

Pugettia gracilis (graceful kelp-crab)

Epialtus productus (Ran.) (decorator crab)

Strongylocentrotus-Pteraster tessalatus association. It is mainly below 36 to 50 meters, down probably to 200 m:

Crossaster papposus (L.) M. & T. (rose star)

Pteraster tessellatus Ives (cushion star)

Gorgonocephalus eucnemis M. & T. (basket star)

Modiolus, Pecten, and barnacles are more abundant, and *Stichopus californicus* is usually less abundant than in the cucumaria community.

h. Succession. Succession probably takes place very rapidly on rock, and the communities may be regarded as at climax. Brandt found that succession required only two years in the Kiel Canal.

The process in the San Juan Channel appears to have been simple but variable in speed. The bottom may be conceived of as smooth rock, with local glacial clay and boulders. The action of the sea, with retreat of the ice, tended to remove the loose materials from the rock in shallow water and deposit them in depressions and pockets and at the bottom. The bottom in the deeper water in places is a sticky blue glacial clay, stiff enough to support sessile animals; in other spots it is sand or occasionally mud. The process which has probably gone hand in hand with the physiographic shifting of bottom materials is the deposition of shells of Pecten, Modiolus, Argobuccinum, etc., on the softer bottom. When these are present barnacles, *Psolus chitonoides*, etc., are found throughout the area under consideration. In other words shells form a substratum similar to rocks or boulders, and the climax fauna spreads throughout as a result of shell bearers living and dead. The phenomena described by Wilson (1925) appear to be seasonal succession or the development of sea-

sonal societies recurring every year. At least such phenomena do recur in northern waters.

i. *Intensive local studies.* The study by Perry (1916), Kirsop (1922), Andrews (1925) and Steggerda & Essex (1925) have had important bearing upon the general conclusions here drawn. The area on which such intensive studies have been made are stippled in Fig. 1 for the work of Andrews on kelp holdfasts and in heavy outline for the other studies. It has required a large amount of observation to establish the *Strongylocentrotus-Argobuccinum* formation. The bottom sampling (Kirsop) and the holdfast work of Andrews showed downward extensions of species formerly supposed to be confined to the shore or nearly so.

j. *History.* Considerable work has been done on the fauna of the shallower subtidal waters of rocky shores but authors have very frequently limited themselves to an area reached from a rowboat or even to the areas exposed at extremely low tides. Nearly all have named depth or algal zones, and the examination of literature proved so unprofitable that it was discontinued, possibly without discovering important but somewhat obscure papers, if such exist. Most authors who have dealt with the subtidal area have not made a distinction between the *Balanus-Littorina* Formation and the formation occupying the subtidal belt. The lower limit of brown algae has been quite generally regarded as important, but in Puget Sound there is little or no difference in this general region. The lower limit of the red algae however shows change in the larger animal life. The hold-fasts of some of the algae seem to be important as hiding places, but no doubt various other places serve the same purpose.

Apellöf's account of the invertebrate bottom fauna in Murray and Hjort (1912) is one of the best faunal accounts. He does not separate the intertidal from the sub-tidal community but calls everything down to 30 or 40 meters the littoral zone and recognizes the sub-littoral zone below this, down to a depth of 150 meters. He makes no use of the idea of dominants.

The senior writer's (1916) suggestions following the usual Forbes classification have proved entirely erroneous. Rocky areas are too infrequent on the coast of Denmark and about Woods Hole to afford opportunity for study.

4. *Pelagic Formation*

This is dominated by altogether different plants and animals than the other communities discussed. Certain small plants, protozoa, and crustacea are doubtless present all the year round and abundant

enough to be considered as dominants, but this has not been ascertained for the Puget Sound waters. This community is no doubt divisible into associations which occupy different depths or regions of different salinity.

There are a number of societies to be recognized among the regular plankton organisms, and also, an important influx from the bottom communities in the form of eggs and young stages. These have not however been studied for the Puget Sound waters. Lebour (1920) has listed the young fishes for each month at Plymouth, England, together with their food. This work indicates something of the kind of larger animals to be expected from month to month. The plankton of the west coast of England (Johnson, 1908, p. 96) shows two major seasonal societies. There are differences in the animals present at different depths, and those taken at different hours at the same depth usually differ (Dice, 1914). The phytoplankton has been discussed by Allen, (1921).

The common larger pelagic fauna of the enclosed waters are the young salmon of all the common species, young herring, eulachon, surf smelt, and jelly-fishes:—*Aequoria* (Weese & Townsend, 1921), *Mitrocoma*, *Phialidium* and *Cyanea arctica* P. & L. apparently occur everywhere in season. Copepods are common and pteropods occur occasionally. There appears to be no definite pelagic regions within San Juan Channel.

The plankton contains the young of the molluscs, barnacles, shrimps, crabs and echinoderms. Some of these serve as food for the young fish (Lebour, 1918). They are widely disseminated but survive only in certain localities. In this respect they are like plants, disseminules, and may be regarded in the same light. However they serve as food for young fishes and thereby are more significant.

Fishes may be regarded as in the class with migratory birds. Some like the herring are pelagic and breed on the bottom, and are accordingly comparable to birds which migrate for breeding. A considerable number of adult fish live at the bottom and feed on the bottom animals. These merely take the place of resident birds.

5. Other Communities

The communities herein described occur thruout the areas thrown into small squares (Fig. 1) except possibly in that of Canoe Island where soft bottom occurs with various clams such as *Psephidia lordi* Baird; *Cardium californiense* Deshayes; *Marcia kennerleyi* (Carpenter) Reeve; *Marcia subdiaphana* Carpenter; *Venericardia ventricosa* Gould; *Mytilimeria nuttallii* Conrad. This may be indicative of other com-

munities where such clams and buried echinoderms occur without the chief dominants of the bottoms here treated, which is the case off Olga. However the dominants of the hard bottom area are present over the surface near Canoe Island and not in the vicinity of Olga.

The Danish workers have mapped the marine bottom communities off northwestern Europe. While the related plankton and fish fauna are not properly correlated, it appears that most of these are entitled to formation rank (Petersen 1913, pp. 4-6; map No. 1). Petersen's map indicates the formation with local patches of forms besides the principal dominants, scattered about. These no doubt are the basis for characterizing associations. In his appendix to the report (1914) he mapped the communities of the eastern North Atlantic. These are doubtless of formation rank. A study of the data shows that these bottom communities are divisible into associations on the basis of dominants.

The maps of Sumner, Osborn and Cole (1911) indicate that Buzzards Bay has a "soft bottom" community, and Vineyard Sound a "hard bottom" (Petersen's sense) community with entirely different dominants. This work was carried on almost at the same time as that of Petersen, and of Petersen and Jensen, who began using the bottom samplers in 1908; and the fact that it is a mere species catalogue with no suggestion, even of quasi-quantitative work, ideas of dominants, etc., shows how little the ideas of modern ecology had reached the ears of American zoologists then or even now. Modern ecology may be stated to be the science of communities, and not a point of view, as Newman has recently stated. Allee's results over the shallower water of the same region suggest also that there are probably two formations.

DISCUSSION

Some fallacious results of the method using the habitat to designate communities instead of the communities themselves may be seen in the case of the "Laminarian Zone." In the case of animals there is no such zone and in about half the territory examined there is no such zone anyway. The Laminariceae are wanting except in patches and the fauna is the same where they are not present as where they are. This is quite necessarily true, because they are seasonal anyway, and when they die, the animals have to live without them. Evidently no important animals are ordinarily limited to them.

The preceding efforts at determining communities on the basis of dominants is to be regarded as tentative, not in principle, but in detail. The results with the bottom sampler (Kirsop 1922) are suffi-

ciently different from those of the dredge, and Petersen has called attention to the great affinity of the dredge for *Strongylocentrotus drobachiensis*, and to the few which the bottom sampler picks up. A full statement of the community relation up to the standard of Clements and Petersen will have to await the study of the plankton, the fish, and further bottom sampling. Fishes and the more active crustacea such as shrimps will probably need to be classified primarily with the area occupied during the breeding season.

The work has been carried far enough to convince the authors that an elaboration of the methods of Petersen as exemplified by the work of plant ecologists (especially Clements) will do much to bring an end to the confusion of long lists and endless confused detail.

The surveys of American waters have been disappointing, because without guiding principle. The aim has been to make as long lists as possible and give more attention to the rare species than to the dominants (Verrill and Smith 1873; Summer, Osburn and Cole 1911; Sumner *et al.* 1914; and contemporary papers) and to the physical conditions which, treated separately, are likely to show very little.

There is no doubt but that the failure of such investigation to arrive at any conclusion is due to a failure to appreciate the meaning of modern ecological methods from a biological viewpoint. At any rate it will be granted that to appreciate the biological relation it is necessary first to find those species which dominate and control the habitat (dominants); second those which are present seasonally and locally and of secondary importance; and finally those which are rare or scarce and of little significance.

The way in which organisms control a habitat is not yet clear except in the case of the dominant trees in our forests. It seems quite impracticable to accept this idea as universal because in the case of the great plains, plant communities may have been held in a subclimax state by the bison; in such a case the control of the community depended upon the bison rather than the climax grasses, though the subclimax grasses are in part directly responsible for the presence of the bison, etc.

There is every reason to combine plant and animal studies and to work on the biota which is the real unit. From the standpoint of animals the facts of distribution have been too little stressed. They are essentially quantitative or must be based upon quantitative data, whereas the usual procedure is essentially qualitative.

On the animal side, in carrying on quantitative work, there are obvious difficulties not encountered among land plants. These are frequently, if not generally due to:

1. The absence of large stationary, obviously dominating animals comparable to trees, shrubs and conspicuous herbs (which throw the smaller fungi, algae, mosses, etc., into insignificance).

2. Animal movement, hiding, etc., especially the differences in habitat of different life history stages.

3. The tendency to use species of restricted range to designate communities, etc., where dominants should be used.

4. The ease with which animal response can be determined and general physiological characters demonstrated.

The difficulties along these lines are less in the case of marine animals. The most important facts of marine animal distribution are similar to those of land plants, and we believe, to those of organisms in general. These facts are determined by the intensive study of small sample areas often when small, called quadrats.

Figure 9 shows in a diagramatic way the manner of distribution of animals in the bottom of San Juan Channel. The basis for two formations is made evident by a complete change in dominants. The narrow strip represents the *Balanus-Littorina* formation with X, Y and Z as most important dominants, .., ** and †† as subdominants.

The wide area represents *Strongylocentrotus-Argobuccinum* Formation. Dominants A, B, C, D, E, F, G are distributed from 0 to 125 m. The restriction of dominants H, I, J, K to the 0-36 m. area, and L, M, N, O to the 36-125 m. area is made evident. This is the basis for two associations.

If we let each letter stand for 10 individuals we see that there are several areas dominated by E, G, O, M, J, etc. These represent mere irregularities such as occur quite generally, and which investigators untrained in ecology call "associations" usually with comment as to their number and variety. These are aggregations which Clements calls "consociations" when climax, or consocieties when developmental.

In connection with Fig. 9 it is necessary to imagine the presence of scores of less abundant and rare species scattered occasionally among the dominants or occurring in small clans or singly. In this paper we have not attempted to list them. Ecologically they are relatively unimportant. Zoologically, i.e., from the standpoint of so-called surveys, they are most important, and as a rule command most interest and attention, especially the rare ones. The rarer the more interesting taxonomically, and the less significant ecologically.

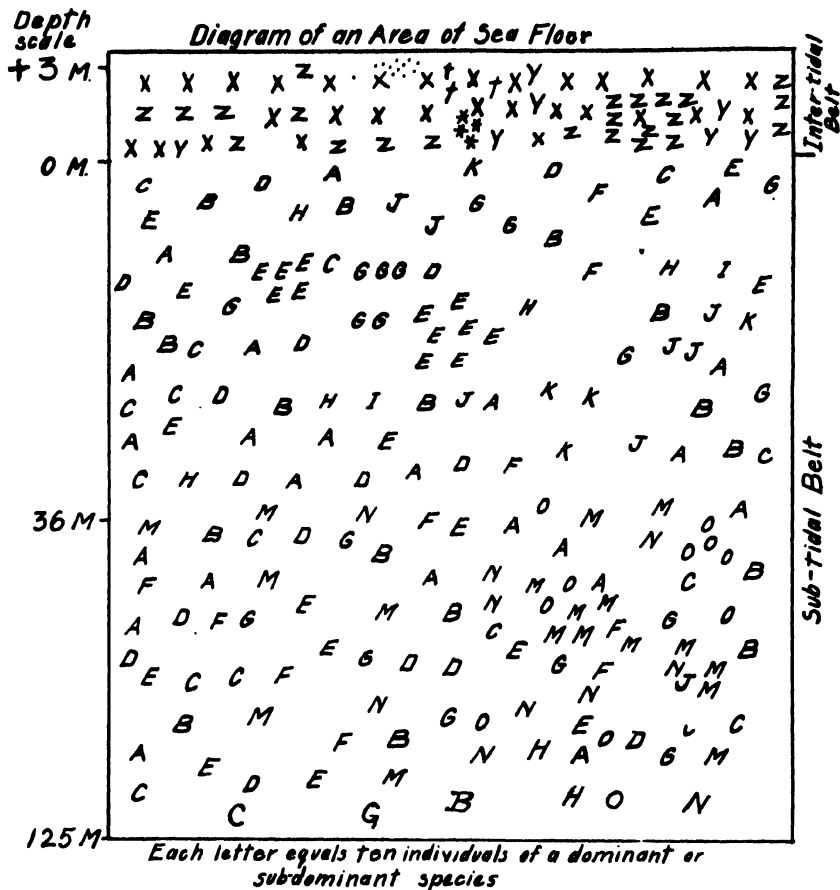


Figure 9. Diagram showing the usual distribution of organisms with especial reference to the sea bottom in San Juan Channel. Letters are used to indicate the animals, each letter understood to indicate several individuals. X, Y, Z, indicate the dominant animals of one community; *† indicate subdominants and secondary species. A, B, C, D, E, F, G, indicate the generally distributed dominants of another community. H, I, J, K, and M, N, O are dominants confined to portions of the area. For further explanations see text.

SUMMARY

1. Communities must be determined by dominants rather than habitat; the limits of the dominants as such are the limits of the community.

2. On the basis of dominants, four extensive communities (formations) occur in San Juan Channel and adjacent waters; these are divisible into associations in which a part of the dominants are different.

The Strongylocentrotus-Argobuccinum formation, for example may be described as follows:

a. It is distributed over most of the bottom of San Juan Channel regardless of bottom materials or with only minor differences correlated with them.

b. It is characterized by two associations one ranging from low tide to about 36 m. and another from about 36 m. to 125 m. or as deep as the investigation was carried.

c. There are minor groupings within the associations such as are called clans, consocieties, consociations, etc., by plant ecologists.

d. Persons untrained in ecology often call these minor groupings associations, and are unable to arrange the communities in order because of confusion of details.

e. The Laminarian belt of Forbes, so long recognized, is without basis as an animal community; the dominant animals are the same where the brown algae are wanting as where they are present.

4. Dominant organisms best illustrate the physiological characters of the community and are the best indicators of the community conditions.

5. Secondary species and uncommon species are of minor significance in ecology (though the chief interest of taxonomy and taxonomic surveys).

6. All the dominants must be considered in the study of communities. Such misnomers as "insect associations," "fish associations" or "mammal associations" should not be tolerated.

7. Seasonal societies must be recognized in all communities but especially in the pelagic community.

8. Succession takes place very rapidly in the sea, a climax probably being reached on hard bottoms in a year or two. Succession is much less rapid on the softer bottoms. The establishment of a hard bottom community on comparatively soft bottom must await the accumulation of shells.

9. Succession in the Macoma formation, after reaching a marine climax, may proceed through a series of retrograde stages to swamp and land. Here succession is accompanied by decreased circulation, and the accumulation of organic matter and decomposition products.

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Larval Trematodes of Certain Marine Gastropods From Puget Sound

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During the course of a survey of the larval trematodes infesting the fresh water snails of San Juan Island (Miller, 1925*b*), opportunities were presented from time to time to examine various of the marine gastropods of the region. Eleven hundred and ninety-three representatives of fifteen species belonging to eleven genera of gastropods, mostly snails, were examined.* The data on the infestation of these mollusks are presented in this paper, together with notes on the morphology of five of the larvae found: a cotylicercous distome, a binocularate gymnocephalous distome, a huge-tailed monostome, and two species of cystophorous larvae. This study is the first to be made of marine cercariae from the Pacific coast of the United States.

The mollusk hosts were collected from the inter-tidal zone on shores close to the biological station, on adjacent islands, and on islands and reefs within a radius of ten miles. Others were dredged in various localities from depths varying from 6 to 30 meters; none of these were infested. The detailed collection records are given in tables 1 and 2; in the latter are grouped the mollusks found to be harboring larval trematodes, with the percentages of infestation. These percentages are actual, as in every case the snails were crushed and examined under a dissecting microscope. Only six species of snails, belonging to five genera, were infested. That none of the remaining nine species were found to harbor trematodes is probably due in part to the fact that large numbers of each were not available, the percentage of infestation of marine mollusks often being quite low.

In the cases of the five cercariae described below an especial effort was made to determine the excretory system pattern, both because this system is completely known for only one marine larva, *Cercaria setifera* (in Monticelli, 1914), and because of the importance attached to it by students of fresh water larvae. It is held that the homologies of this system in cercariae more nearly show the natural relationships of the cercariae (and therefore of the adults) than does

*The author is indebted to Mrs. Ida S. Oldroyd, Curator of the Geology Museum of Leland Stanford University, for identification of representative mollusks.

TABLE 1. Summary of collection and infestation records.*

Mollusk species	Number Ex- amined	Percent of In- festation	Locality
<i>Acmaea cassis pelta</i> Esch.....	26	0	Brown's Is. opposite station
<i>Acmaea scutum patina</i> Esch.....	13	0	Brown's Is. opposite station
<i>Amphissa columbiana</i> Dall.....	49	0	N-W. shore of Henry Is.
<i>Argobuccinum oregonense</i> Redf..	49	0	Dredged off Point Caution
<i>Bittium eschrichtii</i> Midd.....	101	14	(see table 2)
<i>Calliostoma annulatum</i> Martyn..	12	0	Dredged off Point Caution
<i>Calliostoma costatum</i> Martyn...	119	0	(Dredged off Point Caution (Dredged in Pea Vine Pass (N-W. shore of Henry Is.
<i>Calliostoma variegatum</i> Cpr....	6	0	?
<i>Littorina scutulata</i> Gould.....	45	11	(see table 2)
<i>Margarites pupillus</i> Gould.....	44	0	N-W. shore of Henry Is.
<i>Purpura foliata</i> Martyn.....	95	3	(see table 2)
<i>Searlesia dira</i> Reeve.....	254	3	(see table 2)
<i>Thais lamellosa</i> Gmel.....	289	3	(see table 2)
<i>Thais emarginata</i> Desh.....	41	20	(see table 2)
<i>Trichotropis cancellata</i> Hinds...	50	0	(Dredged off Point Caution (N-W. shore of Henry Is.
	1193		

*3.8% of all mollusks infested.

any other organ system of either larva or adult. In the cases of the two cystophorous larvae found during this survey, details of morphology are incomplete due to concentration on the attempt to analyze their excretory systems. The stylet cercariae infesting *Littorina scutulata*, *Searlesia dira*, and *Thais lamellosa* were not studied and it is not known how many species were present. Each of the five larvae studied was specific to its snail host as far as is known; and no cases were found in which a single host individual was infested with more than one species of cercaria. In addition to the study of living parthenitae and larvae, stained total mounts and sections of the three species which are assigned names were used to demonstrate structures not readily seen in the living material. Except where noted, all measurements were made from Canada balsam mounts.

Cercaria purpuracauda spec. nov.
(figs. 1-4)

Cercaria purpuracauda is very similar in many respects to *C. equitator* which Sinitsin (1911) described from *Cerithium exille* from the Black Sea. Both are binoculate monostome larvae, with huge tails many times the length of the body and a close similarity of

bodily organization. *C. purpuracauda* was found in the digestive gland of 12 out of 93 specimens of *Bittium eschrichtii*, a common gastropod of the inter-tidal zone near the Biological Station. In several cases the cercariae were mature, and emerged from the snail host when it was isolated in a vial containing sea water. Partly because of the fact that Sinitsin had described in considerable detail the morphology of *C. equitator* but had not recorded any details of the excretory system, an especial effort was made to determine the pattern of this system in *C. purpuracauda*.

Development takes place in elongate spindle or club-shaped rediae; the latter form is most common in permanent mounts (fig. 4). All stages from early germ balls to cercariae with well formed tails are present. The redia has a minute pharynx, and a short pear-shaped gut which stains deeply with intra-vitam neutral red. A birth pore with a raised lip is present, through which the nearly mature cercariae emerge; further development appears to take place outside of the parthenita, in the lymph spaces of the digestive gland. A redia of average size is 1.3 mm. long and 0.18 mm. in greatest diameter; they may reach 2 mm. in length and 0.3 mm. in diameter.

The prominent oral sucker (fig. 1) is spherical in outline, with the opening directed ventrally, or at times even somewhat posteriorly. A group of nuclei, 14 μ in diameter, probably represents the pharynx; this was the only portion of the alimentary canal observed. A pair of large eye spots, each a mass of brown pigment granules, are in dorsal and posterior connection with the principal nervous tissue mass. They are more irregular in shape than those shown by Sinitsin for *C. equitator*. In addition there may be scattered pigment granules in *C. purpuracauda*, mostly on the anterior half of the body and especially on the dorso-lateral surfaces in the region of the eye spots; there may also be a few scattered granules on the ventral surface. Seven pairs of larval glands take up a great portion of the body, as shown in an individual stained with intra-vitam neutral red (fig. 2); the glands are yellowish in the living cercaria, and eosinophilic in sections. As in *C. foliatae* spec. nov. the ducts are in two separate bundles, a median one of four ducts and a lateral bundle of three ducts on each side. The number of glands and the character of their cytoplasm are not described for *C. equitator*.

The excretory system of *C. purpuracauda* was studied almost continuously for more than a week, in an effort to determine the pattern of the flame cells and tubules; only major tubes and the locations of flame cells were made out (fig. 3). The anterior and posterior

lateral collecting tubules pour into the main lateral collecting tube opposite the germ cell mass; this in turn empties into the thick-walled excretory vesicle. There is some suggestion that most of the flame cells may be grouped in threes. The large mass of nuclei representing the reproductive system corresponds in size and position to that of *C. equitator*; but the line of nuclei leading from it to the vagina, anterior to the oral sucker as figured by Sinitsin, was not observed. On the body there is a short anterior cap of retrorse spines much larger than those farther to the posterior; and those on the tail are still smaller.

The huge tail is used in locomotion through the water or along the surface of a substratum. In such locomotion the body plays little or no part, for it is bent ventrally on the tail in such a way that the oral sucker touches, or almost touches, its surface. The mature cercariae which have emerged swim for a time in all directions through the water, during which they frequently suddenly cease locomotion and sink downwards for short distances. In this sinking they gradually come to a position in which the juncture of body and tail is down, and the tail is held in a more or less straight vertical line. They may come to rest in this position on the bottom, with the tail leaning against the side of the vial. Locomotion along the surface of the substratum consists in an active wriggling, half swimming, serpentine movement effected by the rapid lashing of the tail. This vibration usually results in the formation of three nodes: one at the junction of body and tail, a second in the middle of the tail, and the third at the tip. Progress is always made with the body-tail junction forward, there being no alternation of swimming backwards as is characteristic of certain furcocercous larvae. Frequently there is a great deal of active lashing without any locomotion. A characteristic feature of the tail of *C. purpuracauda* is that it contains numerous pigment granules which give to it a deep purple color, visible to the naked eye.

In permanent mounts the body averages 0.14 mm. in length and 0.06 in width, and the tail is 1.5 mm. in length and 0.13 mm. in greatest diameter. These measurements are somewhat smaller than those for living cercariae.

Cercaria foliatae spec. nov.

(figs. 5-7, 11)

This gymnocephalous distome cercaria was found in 3 out of 68 specimens of *Purpura foliata* from Shaw Island; 27 individuals from three other localities were not infested. All three infestations were

immature, so that only a few fully developed cercariae were available for study; hence the observations are not entirely complete.

Development takes place in elongate rediae found in the lymph spaces of the digestive gland; they are rather uniform in diameter, without locomotor appendages (fig. 11). The largest redia found was 1.2 mm. long and 100μ in diameter. A muscular pharynx and pear-shaped gut are present; the contents of the latter are yellow in the living redia and in total mounts, and strongly eosinophilic in sections. A birth pore, without conspicuous lips, is present.

The oval oral sucker opens antero-ventrally, and is somewhat larger than the ventral sucker. Two eye spots, thick-walled cups formed of small pigment granules, are in antero-dorsal connection with the principal mass of nervous tissue; a small "lens", formed by the nerve ending, is present. Details of the digestive system are extremely difficult to see. The narrow, thin-walled esophagus is surrounded by a pharynx 15μ in diameter, located anterior to the larval glands; from it a short portion of the cecum was traced posteriorly. The larval glands occupy the region from the anterior edge of the ventral sucker to the anterior surface of the excretory vesicle. They are not easily counted in the living cercaria; 14 were present in one series of sections. The ducts are grouped into two bundles, which separately penetrate and traverse the oral sucker; in a few observations on living material three ducts were counted in the lateral and two in the median bundle (fig. 7). The cytoplasm of the glands is weakly basophilic to Delafield's hematoxylin; no organ system for the larva stains with intra-vitam neutral red.

The details of the excretory system pattern were worked out for the anterior and posterior ends of the body, but could not be completely determined for the mid region (fig. 7). The flame cells were probably all seen, but the exact connections of the tubules were not made out. The anterior group contains three units and the two posterior ones two each; from the locations of the middle six flame cells it is possible that they also are grouped in pairs. The excretory vesicle, like that of many other marine cercariae, is very thick walled. The main lateral collecting tube bifurcates lateral to the ventral sucker; just before the larva disintegrates under cover glass pressure a succession of single excretory flagella, along the entire length of the tube, may be seen beating toward the posterior (fig. 7). The reproductive system is represented by two deeply staining masses of cells between the ventral sucker and the excretory vesicle. In ventral view these appear to be broadly connected (fig. 5); in sagittal section (fig. 6) it

is seen that the two masses are joined ventrally by a thick connection, and dorsally by only a thin line of nuclei. No interpretation of the organs represented is ventured.

The anterior end of the body of *C. foliatae* has coarse spines which are very much finer, or altogether absent from the posterior third. The larva is a rapid creeper under a cover glass, even after decaudation. The body when well extended averages 274μ in length and 75μ in width; the tail is over twice as long, 574μ , and is 40μ in its greatest diameter.

Cercaria searlesiae spec. nov.

(figs. 8-10, 14)

This larva was found infesting the digestive gland of *Searlesia* (*Euthria*) *dira*, in two per cent of 254 specimens from several localities. It is a stumpy-tailed form, a member of the group discussed by Dollfus (1914) and designated by him the Cotyllicercous cercariae; in every particular *C. searlesiae* fits in with his characterization of the group. Brief descriptions and figures of the other three members were included in Lebour's (1912) review of the British marine cercariae: *C. linearis* Lespès, *C. pachycerca* Diesing (= *C. brachyura* Lespès), and *C. buccini* Lebour spec. inq. Subsequently Lebour described a larva from *Buccinum undatum* which she believes to be almost certainly that of *Zoogonus viviparus*; no tail is present; "except for the peculiarly modified hind end it fits very well into Dollfus' group (1914) of Cotyllicercous cercariae, which all developed in sporocysts in marine gastropods" (Lebour, 1918:516). No mention is made of *Cercaria inconstans* which Sinitsin (1911) described from sack-like sporocysts infesting *Nassa reticulata* from the Black Sea. This larva is very similar to that which Lebour described; neither mature cercaria has a tail, but in the early stages of *C. inconstans* there is a posterior mass of cells representing a caudal appendage which degenerates (Sinitsin, 1911: figs. 73, 74). Further study of the four or more cotyllicercous larvae found in Tortugas mollusks (Miller, 1925c) may make possible the more precise definition of the Cotyllicercous group.

C. searlesiae develops in almost colorless, sausage-shaped sporocysts which may reach 1.5 mm. in length and 0.2 mm. in diameter; the posterior end is rounded and the anterior tapers to a blunt point (fig. 9). The sporocyst as a whole exhibits considerable motility when first freed from the host tissue, especially the anterior end, which extends forward and is quickly withdrawn, and also sways from side to side. Not more than 40 cercariae were observed in any sporocyst.

The most conspicuous structures in the hyaline larva under low powers of the microscope are the yellow excretory vesicle and caudal glands. The oral sucker is ovoid in shape, 52μ long and 37μ in diameter, while the ventral sucker is circular, with the same diameter, and is situated posterior to the middle of the body. The stylet, with two prominent central points, resembles that of *C. buccini*. Only traces of an alimentary canal were found in the living cercaria; what is probably a pharynx, 13μ in diameter, was seen in sections. Eight larval glands are present, and their ducts, in pairs, open dorsal to the stylet (fig. 10); the glands have little affinity for intra-vitam neutral red and stain lightly with haematoxylin in sections.

The excretory vesicle of *C. searlesiae* agrees with Dollfus' (1914: 684) characterization of this structure for the group of cotyllicercous cercariae: "vessie grande, non bifurquée, occupant presque toute la région postérieure du corps à partir de la ventuose ventrale, sa paroi est formé d'une seule couche de très grandes cellules juxtaposées, à contenu granuleux, à aspect glandulaire". The main lateral collecting tube, which receives the anterior and the posterior collecting tubules lateral to the ventral sucker, enters the excretory vesicle antero-laterally. The excretory system pattern was determined for all but the region lateral to the vesicle (fig. 10). The two posterior flame cells were frequently seen just before the larva disintegrated under cover glass pressure; in repeated studies the tubules leading from these cells were not seen. There is a possibility, by a doubtfully positive observation, of an eighth flame cell at the level of the anterior end of the excretory vesicle; in this event the flame cells on either side of the body are probably arranged in four pairs, with two pairs draining into the anterior and two pairs into the posterior collecting tubule. Thus the dichotomy of the two original flame cells, one on either side of the germ ball, has proceeded at the same rate in both the anterior and posterior half of the system, up to the stage represented by the mature cercaria. The flame cell pattern has not been described for other members of this group, so no comparisons can be made.

Two prominent masses of nuclei, somewhat triangular in outline, probably represent the reproductive system. The first is located posterior to the larval glands, with the apex of the triangle pointing posteriorly, and joined by a line of deeply staining nuclei to the posterior mass which lies between the ventral sucker and the excretory vesicle. The tail of *C. searlesiae*, like that of other members of the group, is in the form of a cup with the opening directed posteriorly, and may function like a sucker. Its form varies, but it is never so short and

broad as that shown for *C. brachyura* (in Lebour, 1912: Pl. XXVII, fig. 16). The large cells which fill it are bright yellow even in haematoxylin stained mounts, and are very strongly eosinophilic in sectioned material. The body of *C. searlesiae* is only slightly larger than that of *C. brachyura*, but much smaller than that of *C. buccini*. It averages 248μ in length and 52μ in width; extremely extended specimens may be 326μ long and 33μ wide. The tail which is also capable of considerable changes in size averages 52μ in length and 30μ in width.

Cystophorous cercariae

This note will serve to record the presence in Puget Sound mollusks of two of these larvae, one (*A*) in *Thais emarginata* and the other (*B*) in *Thais lamellosa*. Previously but four marine members of the group have been described: *C. appendiculata* and *C. vaullegeari* by Pelseneer (1906) from the west coast of Europe, and *C. sagittarius* and *C. laqueator* by Sinitsin (1911) from the Black Sea. One other marine cystophorous form was recently found by the author at the Dry Tortugas (Miller, 1925c). The morphology and relationships of the members of the group, including the fresh water forms, were discussed by Cort and Nichols (1920) in connection with their description of *C. californiensis*. There are now ten fresh water representatives, some of which are known only in scanty detail.

The body of the cystophorous cercaria is but little differentiated. Of the excretory system only the main trunks have been observed in the bodies of three larvae, *C. laqueator*, *C. californiensis*, and *C. introverta* (Faust, 1924), although the tubules in the tail and in the tail appendages were more easily traced. Neither of the two Puget Sound larvae was studied in sufficient detail to describe it completely, and accordingly they are designated A and B. An especial effort was made to determine the degree of excretory system development.

The first larva, *A*, from *Thais emarginata*, was found in 8 out of 23 snails collected near the new Station dock and was not present in 18 from another locality. One very small motionless flame cell was found on either side of the body of the cercaria in the cyst. The fine excretory tubules pour into an elongate excretory vesicle which is much enlarged posteriorly (fig. 13). In one individual squeezed out of a cyst two flame cells were observed on each side of the body; a tubule was traced farther anteriorly, but no flame cells were observed in connection with it. In many individuals studied no parts of the excretory system could be found. Development takes place in elongate sporocysts, with constricted areas at infrequent intervals; the

largest measured was 6.5 mm. in length and 0.16 mm. in diameter of the swollen areas. The developmental stages of both this and the larva (*B*) found in *Thais lamellosa* are superficially much like those of the other four marine larvae. Two appendages are present in *A*, one corresponding to the "arrow" of *C. sagittarius* (Sinitsin, 1911: fig. 26*b*) and the other to the "ribbon" (fig. 26*a*); the latter is short and club-shaped, and is located near the juncture of body and sphere of the tail. The diameter of the cyst (fig. 13) in preserved material averages 76 μ ; its size, structure, and the coiling of the body within it are clearly different from that of the other cystophorous larva, *B*, found in *Thais lamellosa*. The latter was immature in three out of four infestations. The cyst (fig. 15) is 60 μ in diameter. Only one caudal appendage, corresponding to the "arrow" of Sinitsin, is present.

TABLE 2. Collection and infestation record of snails harboring larval trematodes.

Snail Host and Locality	Date	Number Collected	Infestations	Percent of Infestation
<i>Bitium eschrichtii</i>				
Shore west of station dock..	June 17	8	1, immature redia.....	13
Brown's Is. opposite station.	June 18	20	5, <i>Cercaria purpuracauda</i>	25
Brown's Is. opposite station.	June 28	73	7, <i>Cercaria purpuracauda</i>	10
			1, unidentified young sporocyst.....	1
<i>Littorina scutulata</i>				
Shore west of dock.....	June 16	45	4, stylet cercaria.....	9
			1, immature sporocyst.....	3
<i>Purpura foliata</i>				
Dredged off Point Caution..	June 21	5	0	0
N-W. shore of Henry Island	Aug. 1	18	0	0
Parker's reef.....	Aug. 3	4	0	0
Shaw Island, opposite Point Caution.....	Aug. 5	68	3, <i>Cercaria foliatae</i>	4
<i>Searlesia dira</i>				
Brown's Is. opposite station.	June 18	95	3, <i>Cercaria searlesiae</i>	3
Cattle Point.....	June 22	7	0	0
Brown's Is. opposite station.	July 31	96	1, immature stylet cercaria...	1
N-W. shore of Henry Is. ...	Aug. 1	56	2, <i>Cercaria searlesiae</i>	4
<i>Thais emarginata</i>				
Cattle Point.....	June 22	18	0	0
Shore east of station dock..	July 1	23	8, cystophorous (<i>B</i>) cercaria...	35
<i>Thais lamellosa</i>				
Brown's Is. opposite station.	June 18	239	3, cystophorous (<i>A</i>) cercaria..	1
			4, micro-stylet cercaria.....	2
Cattle Point.....	June 22	32	0	0
Brown's Is. opposite station.	July 31	18	1, cystophorous (<i>A</i>) cercaria...	6

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1920. Cort, W. W., and Nichols, E. B. A new cystophorous cercaria from California. Jour. Paras., 7:8-15; 1 text fig.
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- 1925a. Miller, H. M. Jr. A survey of the marine gastropods from the vicinity of San Juan Island, Puget Sound, with respect to larval trematode infestation. Abstr. in Anat. Rec., 29:123.

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- 1925c. ————— Preliminary report on the larval trematodes infesting certain mollusks from Dry Tortugas. (In press, Yearbook of the Carnegie Institution of Washington).

PLATE 3

Except where noted, all figures were drawn with the aid of a camera lucida.

The values of the scale lines are expressed in micra.

- Fig. 1 Lateral view of entire *Cercaria purpuracauda*. $\times 90$
Fig. 2 *C. purpuracauda*; dorsal view of body showing distribution of larval glands, deeply stained with intra-vitam neutral red. $\times 230$
Fig. 3 *C. purpuracauda*; freehand sketch of excretory system combined from numerous observations; eye spots and beginnings of reproductive system also shown. $\times 410$
Fig. 4 Club-shaped redia of *C. purpuracauda*; pharynx, pear-shaped gut, and birth pore. $\times 50$
Fig. 5 *Cercaria foliatae*; general view showing pharynx, larval glands, and beginnings of reproductive system. $\times 105$
Fig. 6 Sagittal section of *C. foliatae* through larval glands, reproductive system, and excretory vesicle. $\times 210$
Fig. 7 *C. foliatae*; freehand sketch of excretory system; excretory flagella in main lateral collecting tube and anterior portions of two bundles of larval gland ducts shown on one side. $\times 200$

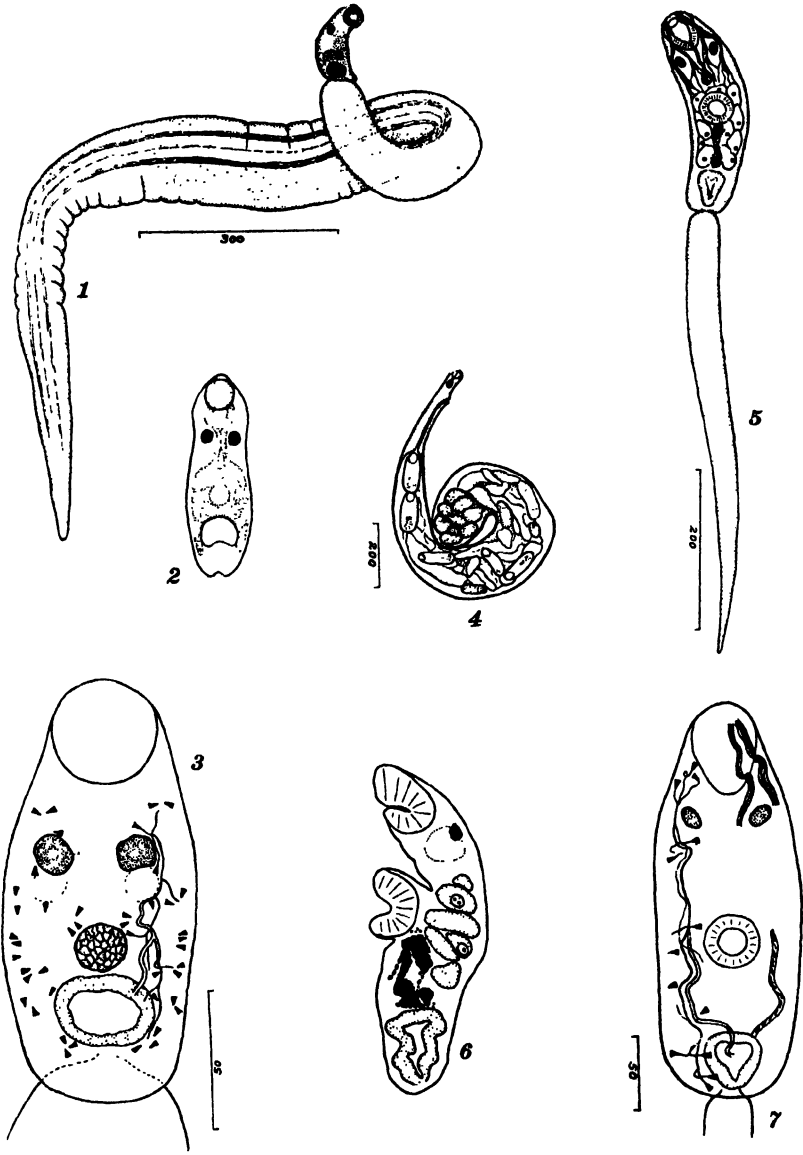


PLATE 3

PLATE 4

Except where noted, all figures were drawn with the aid of a camera lucida.

The values of the scale lines are expressed in micra.

- Fig. 8 *C. searlesiae*; lateral view showing stylet, larval glands, excretory vesicle, and beginnings of reproductive system; ventral sucker withdrawn into body. $\times 330$
- Fig. 9 Sporocyst of *C. searlesiae*. $\times 55$
- Fig. 10 Ventral view of *C. searlesiae*; stylet, larval glands, alimentary, reproductive, and excretory systems shown. $\times 330$
- Fig. 11 *C. foliatae*; redia, with birth pore. $\times 55$
- Fig. 12 Cystophorous cercaria *A*, from *Thais emarginata*; ventral view of body showing alimentary canal and the only part of excretory system observed. \times about 260
- Fig. 13 Cyst of the same species; excretory system in cercaria shown. $\times 560$
- Fig. 14 *C. searlesiae*; lateral outline, body contracted with ventral sucker protruding. $\times 135$
- Fig. 15 Cystophorous cercaria *B*, from *Thais lamellosa*; cyst. $\times 760$

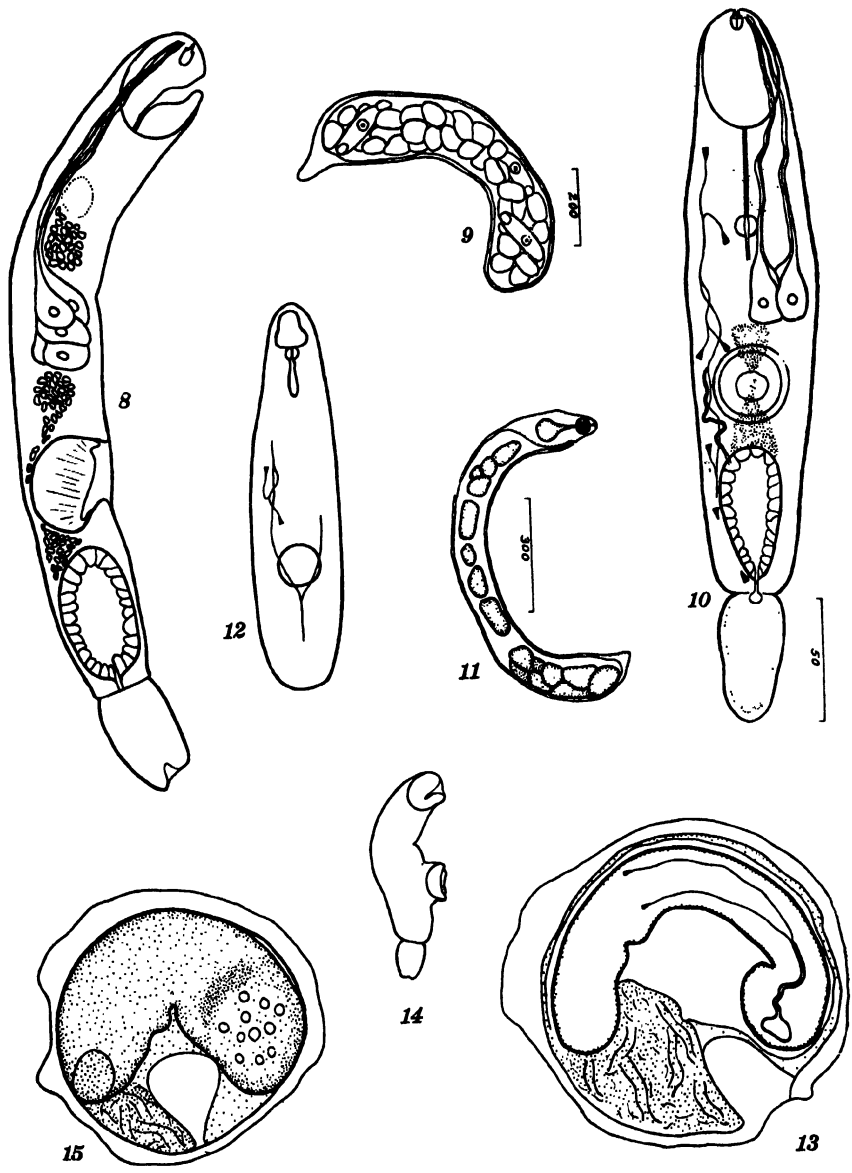


PLATE 4

List of Bryozoa from the Vicinity of Puget Sound

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and

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The following is a list of the Bryozoa which have been recorded from the vicinity of the San Juan Islands and Puget Sound. It is published in order to provide data for the study of the distribution of these forms and also in the hope that it may assist and encourage others in the study of this group. The records at present available are to be found in a series of papers by Robertson (1900-1910) and two by the present authors (1923-1926). These, together with a number of specimens collected by ourselves, and others in the possession of the University of Washington which were kindly sent us for examination by Professor Trevor Kincaid with his customary courtesy, form the basis of the present list. As far as we know the only attempt to collect and identify material from this region has been made by ourselves. In 1921 a few hours spent at Friday Harbor enabled one of us (C. H. O'D.) to secure examples of 19 species with two further varieties of one of them. Two years later we were able to carry out some dredging in Griffin Bay and off Point Caution. The former yielded 35 species and one variety, while four hauls at the latter place produced 76 species and one variety, a truly remarkable number for one locality in so short a time. The two collections are sufficient to show the fertility of the region and to encourage the belief that systematic collecting would add very substantially to the present list.

Apart from a paper by Hincks (1884) the work on forms from the Pacific Coast of North America has been almost exclusively by Robertson and ourselves. The most readily available fundamental source of information on living Bryozoa in the English language is to be found in the works of Busk (1852-1886) and Hincks (1880-1884). The works of these authors, of Robertson and the first of our papers, are arranged according to the classification elaborated by the first two named. More recent work by a number of authorities in Europe has

altered this classification in a very radical manner. The recent system, as applied to fossil species in particular but in part also to recent forms, is to be found in the splendid volumes of Canu and Bassler (1920-1923). The arrangement and nomenclature employed by these authorities has been utilized here as far as possible.

Wherever possible the name of the genus is followed by that of the genotype. In each case, with the name of the species, is given the original citation, followed by the subsequent records in papers dealing with the Pacific Coast of North America. In the latter, in practically all instances, will be found a figure and description of the species, or if not, a reference to a work where such can be found. The locality is given when available but in some cases U.W.C. alone is put to indicate that the record is based on a specimen in the University of Washington collection presumably from the Friday Harbor region.

We desire to express our thanks to the Biological Board of Canada from whose Station at Nanaimo our collecting was done and a certain number of identifications made.

BRYOZOA Ehrenberg (POLYZOA J. V. Thompson)

Sub-class ENTOPROCTA Nitsche 1869

Order PEDICELLINEAE Hincks 1880

Family PEDICELLINIDAE Hincks 1880

BARENTSIA Hincks 1880. Genotype, *Barentsia bulbosa* Hincks 1880.

Barentsia gracilis var *nodosa* Lomas in Proc. Liverpool Lit. Phil. Soc. No. XL: 190, pl. III, 1886. O'Donoghue & O'Donoghue (1923: 147 and 1926).—Griffin Bay, 15-23 meters.

Barentsia parva (O'Donoghue & O'Donoghue), as *Gonypodaria parva* in Contr. Canadian Biol. 1923:148, pl. I, figs. 1a and 1b. Ibid. (1926).—Friday Harbor and Griffin Bay, 15-23 meters.

Barentsia ramosa (Robertson), as *Gonypodaria ramosa* in Proc. Calif. Acad. Sci. II:337, pl. XVI, figs. 13-16, 1900. O'Donoghue & O'Donoghue (1923:148 and 1926).—Channel Rocks, Puget Sound. U.W.C.

Sub-class ECTOPROCTA Nitsche 1869

Super-order PHYLACTOLAEMATA (All in fresh water; not included)

Super-order GYMNOLOEMATA Allman 1856

Order CTENOSTOMATA Busk 1852

Family ALCYONIDIIDAE Hincks 1880

ALCYONIDIUM Lamouroux 1821. Genotype, *Alcyonidium gelatinosum* (Linnaeus) 1767.

Alcyonidium gelatinosum (Linnaeus), as *Alcyonidium gelatinosum* in Linn. Syst. Nat. ed. 12, p. 1295, 1767. Robertson (1902); O'Donoghue & O'Donoghue (1923:191). —U.W.C.

Family VESICULARIIDAE Hincks 1880

BOWERBANKIA Farre 1837. Genotype, *Bowerbankia densa* Farre 1837. *Bowerbankia gracilis* Leidy, in Jour. Acad. Nat. Sci. Philadelphia III: 142, 1855. O'Donoghue & O'Donoghue (1923:192).—Friday Harbor and Griffin Bay, 15-23 meters.

Bowerbankia imbricata (Adams), as *Sertularia imbricata* in Trans. Linn. Soc. II, pl. 2, figs. 5-11, 1798.—U.W.C. A specimen bearing this label is included in the University of Washington collection but it is in such a shrivelled condition that we have been unable to identify it.

Order CYCLOSTOMATA Busk 1852

Division INOVICELLATA

Family DIASTOPORIDAE Gregory 1899

STOMATOPORA Bronn 1825. Genotype, *Stomatopora dichotoma* Lamouroux 1821.

Stomatopora granulata (Milne-Edwards) as *Alecto granulata* in Mem. 13. pl. XVI, figs. 3 and 3a. O'Donoghue & O'Donoghue (1923: 153 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

PROBOSCINA Audouin 1826.

Proboscina diastoporides (Norman), as *Stomatopora diastoporides* in Rept. Brit. Assoc. for 1867, p. 310, 1868. O'Donoghue & O'Donoghue (1923:153, 1926).—San Juan Channel, off Point Caution, 40-45 meters.

Proboscina fasciculata (Hincks), as *Stomatopora fasciculata* in Hist. Brit. Marine Polyzoa, p. 441, pl. LXI, figs. 4 and 5, 1880. O'Donoghue & O'Donoghue (1926).—San Juan Channel, off Point Caution, 40-45 meters.

Division OVICELLATA

Sub-division PARALIELATA Waters 1887

Family CRISIIDAE Johnston 1847

CRISIA Lamouroux 1812. Genotype, *Crisia* (*Sertularia*) *eburnea* Linnaeus 1758.

- Crisia geniculata* Milne-Edwards, in Ann. Sci. Nat. Zool. 2:9:197, pl. 6, fig. 1, 1838. Robertson (1910:235); O'Donoghue & O'Donoghue (1923:149 and 1926).—San Juan Channel, off Point Caution, 40-45 meters. U.W.C.
- Crisia occidentalis* Trask, in Proc. Calif. Acad. Sci. 1:113, pl. 5, fig. 4, 1857. Robertson (1910:239); O'Donoghue & O'Donoghue (1923:149 and 1926).—San Juan Channel; Copalis Rocks. U.W.C.
- Crisia pugeti* Robertson, in Pub. Univ. Calif. Zool. 2:244, pl. 20, figs. 20-21, 1910. O'Donoghue & O'Donoghue (1923:150 and 1926).—Friday Harbor.
- CRISIDIA Milne-Edwards 1838. Genotype, *Crisidia* (*Sertularia*) *cornuta* Linnaeus 1758.
- Crisidia edwardsiana* d'Orbigny, in Voy. dans l'Amer. merid. 5:8, pl. 1, figs. 4-8, 1839. Robertson (1910:237, pl. 19, figs. 9 and 10); O'Donoghue & O'Donoghue (1926).—Channel Rocks, Puget Sound; Friday Harbor and Griffin Bay; low tide to 23 meters.
- Crisidia franciscana* (Robertson), as *Crisia franciscana* in Pub. Univ. Calif. Zool. 2:233, pl. 18, figs. 1-4, 1910. O'Donoghue & O'Donoghue (1926).—Puget Sound.

Family MECYNOECIDAE Canu 1918

- MICROECIA Canu 1918. Genotype, *Microecia* (*Diastopora*) *sarniensis* (Norman) 1864.
- Microecia sarniensis* (Norman) as *Diastopora sarniensis* in Ann. Nat. Hist. ser. 3, XIII:89, pl. XI, figs. 4-6, 1864. O'Donoghue & O'Donoghue (1926).—San Juan Channel, off Point Caution, 40-45 meters.

Family DIAPEROECIDAE Canu 1918

- DIAPEROECIA Canu 1918. Genotype, *Diaperoecia* (*Entalophora*) *intricaria* Busk 1875.
- Diaperoecia capitata* (Robertson), as *Entalophora capitata* in Proc. Wash. Acad. Sci. 2:328, pl. XXI, fig. 12, 1900. Robertson (1910:257, pl. 24, figs. 44 and 45); O'Donoghue & O'Donoghue (1923:155 and 1926).—Friday Harbor. U.W.C.?
- Diaperoecia clavata* (Busk), as *Pustulopora clavata* in Crag Polyzoa, p. 107, pl. XVII, fig. 1, 1859. O'Donoghue & O'Donoghue (1923:155 and 1926).—San Juan Channel, off Point Caution, 40-45 meters.
- Diaperoecia depressa* (O'Donoghue & O'Donoghue), as *Stomatopora depressa* in Contr. Canadian Biol. 1923:153, pl. 1, fig. 5. O'Donoghue & O'Donoghue (1926).—San Juan Channel, off Point Caution, 40-45 meters.

Diaperoecia johnstoni (Heller), as *Criserpia johnstoni* in Bryoz. adriatisches Meeres, p. 50, 1867. O'Donoghue & O'Donoghue (1923: 11 and 1926).—San Juan Channel, off Point Caution, 40-45 meters.

DIPLOSOLEN Canu 1918. Genotype, *Diplosolen* (*Tubulipora*) *obelina* Johnston 1847.

Diplosolen obelium (Johnston), as *Tubulipora obelia* in Brit. Zooph. ed. I, p. 269, pl. XXXVIII, figs. 7 and 8, 1848. O'Donoghue & O'Donoghue (1923:156 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Family TUBULIPORIDÆ Johnston 1838

TUBULIPORA Lamarck 1816. Genotype, *Tubulipora* (*Tubipora*) *flabellaris* Fabricius 1780.

Tubulipora flabellaris (Fabricius), as *Tubipora flabellaris* in Fauna Groenlandica, p. 430, 1780. Robertson (1910:247, pl. 21, figs. 25 and 26); O'Donoghue & O'Donoghue (1923:150).—Channel Rocks, Puget Sound.

Tubulipora fasciculifera Hincks, in Ann. Mag. Nat. Hist. ser. 5, 13: 206, 1884; O'Donoghue & O'Donoghue (1923:8 and 1926).—Friday Harbor. U.W.C.?

Tubulipora pulchra MacGillivray, in Trans. Proc. Roy. Soc. Victoria XXI:94, pl. 2, fig. 1, 1885. Robertson (1910:250, pl. 23, figs. 32-35); O'Donoghue & O'Donoghue (1923:150 and 1926).—U. W.C.

Tubulipora serpens (Linn.) var. *radiata* Hincks, as *Tubipora serpens* Linn. Syst. Nat. ed. 12, 1767, var. *radiata* Hincks, in Brit. Marine Polyzoa p. 453, pl. LXI, figs. 2-3, and pl. LX, fig. 2, 1880. O'Donoghue & O'Donoghue (1923:150 and 1926).—San Juan Channel, off Point Caution, 40-45 meters.

Tubulipora tuba (Gabb & Horn), as *Semitubigera tuba* in Jour. Acad. Nat. Sci. Philadelphia ser. 2:V:169, pl. XXI, fig. 57, 1862. O'Donoghue & O'Donoghue (1926). As *T. occidentalis* Robertson (1910:249); O'Donoghue & O'Donoghue (1923:150).—Puget Sound and San Juan Channel, off Point Caution, 40-45 meters.

Family CYTISIDÆ d'Orbigny 1854

DISCOCYTIS d'Orbigny 1854. Genotype, *Discocytis* (*Pelagia*) *eudesi* Michelin 1844.

Discocytis canadensis O'Donoghue & O'Donoghue, in Contr. Canadian Biol. 1926. As *Supercytis digitata* O'Donoghue & O'Donoghue (1923:158).—Friday Harbor and San Juan Channel, off Point Caution, 40-45 meters. U.W.C.

Sub-division RECTANGULATA Waters 1887

Family LICHENOPORIDAE Smitt 1866

LICHENOPORA DeFrance 1823. Genotype, *Lichenopora* (*Discopora*) *hispida* Fleming 1828.

Lichenopora hispida (Fleming), as *Discopora hispida* in Brit. Anim. 1828:530. Hincks (1884:36); O'Donoghue & O'Donoghue (1923:157 and 1926).—San Juan Channel, off Point Caution, 40-45 meters.

Lichenopora fava O'Donoghue & O'Donoghue, in Contr. Canadian Biol. 16, pl. 1, fig. 9, 1923. Ibid. (1926).—San Juan Channel, off Point Caution, 40-45 meters.

Lichenopora verrucaria (Fabricius), as *Madrepore verrucaria* in Faun. Groenlandica, p. 430, 1780. Hincks (1884:36); Robertson, (1910:263, pl. 25, fig. 50); O'Donoghue & O'Donoghue (1923:157 and 1926).—San Juan Channel, off Point Caution, 40-45 meters.

TRETOCYCLOECIA Canu 1919. Genotype, *Tretocycloecia* (*Heteropora*) *dichotoma* Reuss 1847.

Tretocycloecia pelliculata (Waters), as *Heteropora pelliculata* in Jour. Roy. Mic. Soc. 2:390, pl. 15, figs. 1-4 and 7, 1879. Robertson (1910:258, pl. 25, figs. 51-55); O'Donoghue & O'Donoghue (1923:156 and 1926).—San Juan Channel, off Point Caution, 40-45 meters.

Order TREPANOSOMATA (All palaeozoic, not included)

Order CRYPTOSOMATA (All palaeozoic, not included)

Order CHELOSOMATA Busk

Sub-order ANASCA Levinsen

Division MALACOSTEGA Levinsen 1909

Family ELECTRINIDAE d'Orbigny 1851

MEMBRANIPORA Blainville 1834. Genotype, *Membranipora* (*Flustra*) *membranacea* Linnaeus 1767.

Membranipora membranacea Linnaeus, as *Flustra membranacea* in Syst. Nat. ed. 12, p. 1301, 1767. Hincks (1884:11); Robertson (1908:267, pl. 16, figs. 19, 19a, 20); O'Donoghue & O'Donoghue (1923:168).—Puget Sound; Copalis Rocks. U.W.C.

Membranipora serrata (Hincks), as *Membranipora membranacea* form *serrata* in Ann. Mag. Nat. Hist. 1:469, 1882. Robertson (1908:268, pl. 16, figs. 20, 21, 21a); O'Donoghue & O'Donoghue (1923:168 and 1926).—Puget Sound; Friday Harbor; Griffin Bay and San Juan Channel, off Point Caution; low tide to 45 meters.

- Membranipora villosa* Hincks, in Ann. Nat. Hist. 6:84, pl. 10, fig. 8, 1880. Robertson (1908:269, pl. 16, figs. 24a, 24b, and 25); O'Donoghue & O'Donoghue (1923:168 and 1926).—Puget Sound; Friday Harbor; Griffin Bay and San Juan Channel, off Point Caution; low tide to 45 meters.
- HINCKSINA Norman 1903. Genotype, *Hincksina* (*Membranipora*) *flustroides* Hincks 1880.
- Hincksina pallida* (Hincks), as *Membranipora pallida* form *multispinata* in Ann. Mag. Nat. Hist. 10:39, pl. XIX, fig. 4, 1882. O'Donoghue & O'Donoghue (1923:167 and 1926).—Friday Harbor; Griffin Bay and San Juan Channel off Point Caution, 15-45 meters.
- CALLOPORA Gray 1848. Genotype, *Callopora* (*Membranipora*) *lineata* (Linnaeus) 1758.
- Callopora brevispina* O'Donoghue & O'Donoghue in Contr. Canadian Biol. (1926), as *Membranipora lacroixii* var. *triangulata* ibid. (1923:167).—Friday Harbor.
- Callopora circumclathrata* (Hincks), as *Membranipora circumclathrata* in Ann. Mag. Nat. Hist. 8:131, pl. 5, fig. 1, 1881. Robertson (1908:259, pl. 14, figs. 1, 2); O'Donoghue & O'Donoghue (1923:166 and 1926).—Griffin Bay and San Juan Channel off Point Caution, 15-45 meters.
- Callopora horrida* (Hincks), as *Membranipora horrida* in Ann. Mag. Nat. Hist. 6:32, pl. 10, fig. 6, 1880. Robertson (1908:260, pl. 14, figs. 3, 4); O'Donoghue & O'Donoghue (1923:166 and 1926).—Puget Sound; Friday Harbor; Griffin Bay and San Juan Channel off Point Caution; low tide to 45 meters.
- AMPHIBLESTRUM Gray 1848. Genotype, *Amphiblestrum* (*Membranipora*) *flemingii* Busk 1852.
- Amphiblestrum alaicorne* (O'Donoghue & O'Donoghue), as *Membranipora alaicornis* in Contr. Canadian Biol. p. 168, pl. II, fig. 14, 1923. Ibid. (1926).—Friday Harbor; Griffin Bay and San Juan Channel off Point Caution, 15-45 meters.
- Amphiblestrum patulum* (Hincks), as *Membranipora patula* in Ann. Mag. Nat. Hist. 7:150, pl. 9, fig. 5, 1881. Robertson (1908:253, pl. 15, fig. 10). O'Donoghue & O'Donoghue (1923:167, and 1926).—Friday Harbor, and San Juan Channel off Point Caution, 40-45 meters.
- CAULORAMPHUS Norman 1903. Genotype, *Cauloramphus* (*Flustra*) *spinifer* (Johnston) 1832.

Cauloramphus spinifer (Johnston), as *Flustra spinifera* in Trans. Nat. Hist. Soc. Northumberland 2:266, pl. 9, fig. o, 1832. Robertson (1908:265, pl. 15, fig. 15); O'Donoghue & O'Donoghue (1923:168 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Family AETEIDAE Smitt 1867

AETEA Lamouroux 1812. Genotype, *Aetea (Sertularia) anguina* (Linnaeus) 1758.

Aetea truncata (Landsborough), as *Anguinaria truncata* in Hist. Brit. Zooph. p. 228, pl. XVI, fig. 57, 1852. Robertson (1905:246, pl. IV, fig. 5, 6); O'Donoghue & O'Donoghue (1923:158 and 1926).—Friday Harbor; San Juan Channel off Point Caution, 40-45 meters.

Family SCRUPOCELLARIIDAE Levinsen 1909

SCRUPOCELLARIA Van Beneden 1845. Genotype, *Scrupocellaria (Sertularia) scruposa* Linnaeus 1758.

Scrupocellaria californica Trask, in Proc. Calif. Acad. Sci. 1:114, pl. 4, fig. 2, 1857. Robertson (1905:259, pl. VIII, figs. 35, 36, 36a, 37); O'Donoghue & O'Donoghue (1923:160 and 1926).—Friday Harbor and Griffin Bay, 15-23 meters.

Scrupocellaria varians Hincks, in Ann. Mag. Nat. Hist. 10:461, pl. XIX, figs. 1-1c, 1882. Robertson (1905:260, pl. VIII, figs. 38, 39 and pl. XVI, fig. 95); O'Donoghue & O'Donoghue (1923:160 and 1926).—Copalis Rocks; Channel Rocks, Puget Sound and San Juan Channel, off Point Caution; low tide to 45 meters. U. W.C.

CABEREA Lamouroux 1816. Genotype, *Caberea dichotoma* Lamouroux 1816.

Caberea ellisii (Fleming), as *Flustra ellisii* in Mon. Wer. Soc. 2:251, 1828. Robertson (1905:263, pl. V, figs. 12-16, and pl. VI, fig. 17); O'Donoghue & O'Donoghue (1923:161 and 1926).—U.W.C., Deer Harbor and San Juan Channel off Point Caution, 40-45 meters.

MENIPEA Lamouroux 1812. Genotype, *Menipea (Cellularia) crispa* (Pallas) 1766.

Menipea erecta Robertson, in Proc. Wash. Acad. Sci. 2:317, pl. XIX, figs. 1 and 2, 1900. Robertson (1905:256, pl. VII, figs. 28-31); O'Donoghue & O'Donoghue (1923:160 and 1926).—Puget Sound; Friday Harbor; Griffin Bay, San Juan Channel off Point Caution; 15-45 meters.

- Menipea gracilis* Busk, in Jour. Linn. Soc. V, 1881. Robertson (1905:253, pl. VI, figs. 18-21); O'Donoghue & O'Donoghue (1923:160 and 1926).—San Juan Channel off Point Caution, 40-45 meters.
- Menipea occidentalis* Trask, in Proc. Calif. Acad. Sci. 1:113, pl. IV, fig. 4, 1857. Robertson (1905:254, pl. VI, figs. 22-25); O'Donoghue & O'Donoghue (1923:159).—Stated by Robertson to occur from Queen Charlotte Islands to San Diego.
- Menipea pribilofi* Robertson, in Univ. Calif. Pub. Zool. 2:257, pl. VII, figs. 32, 33, and pl. VIII, fig. 34, 1905.—U.W.C. This material may not have been collected locally but may have been left with other Alaskan specimens by Dr. Alice Robertson.
- Menipea ternata* (Ellis & Solander), in Nat. Hist. Zooph. p. 208, pl. 63, 1786. Hincks (1884:37); Robertson (1905:251, pl. V, figs. 12-16, and pl. VI, fig. 17); O'Donoghue & O'Donoghue (1923:159 and 1926).—Copalis; Channel Rocks; San Juan Island and Griffin Bay; 15-23 meters.

Family BICELLARIIDAE Smitt 1867

- BICELLARIELLA Levinsen 1909. Genotype, *Bicellariella* (*Sertularia*) *ciliata* (Linnaeus) 1758.
- Bicellariella stolonifera* O'Donoghue & O'Donoghue, in Contr. Canadian Biol. 1926.—Griffin Bay, 15-23 meters.
- BUGULA Oken 1815. Genotype, *Bugula* (*Sertularia*) *neritina* (Linnaeus) 1758.
- Bugula cucullifera* Osburn, in Bull. U.S. Bur. Fish. XXX:225, pl. XXII, figs. 24, 24a-c, 1910. O'Donoghue & O'Donoghue (1923:164 and 1926).—Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters.
- Bugula curvirostrata* Robertson, in Univ. Calif. Pub. Zool. 2:272, pl. XI, figs. 56-58, 1905. O'Donoghue & O'Donoghue (1923:163 and 1926).—San Juan Channel off Point Caution, 40-45 meters.
- Bugula laxa* Robertson, in Univ. Calif. Pub. Zool. 2:275, pl. XII, figs. 61 and 62, 1905. O'Donoghue & O'Donoghue (1923:163 and 1926).—Puget Sound, Channel Rocks. U.W.C.
- Bugula murrayana* (Johnston), as *Flustra murrayana* in Brit. Zooph. ed. 2, p. 347, pl. LXIII, figs. 5 and 6, 1847. Robertson (1905:266, pl. X, fig. 48 and pl. XVI, figs. 98, 99); O'Donoghue & O'Donoghue (1923:162 and 1926); Hincks (1884:6).—Friday Harbor and Puget Sound. U.W.C.

Bugula pacifica Robertson, in Proc. Wash. Acad. Sci. 2:321, 1900, also as *Bugula purpurotincta* ibid. p. 320. Robertson (1923:268, pl. X, fig. 50, and pl. XVI, fig. 101); O'Donoghue & O'Donoghue (1923:162 and 1926.—U.W.C. Roche Harbor; Sidney; Puget Sound and Channel Rocks.

Bugula pugeti Robertson, in Univ. Calif. Pub. Zool. 2:271, 1905, pl. X, figs. 53, 54, and pl. XI, fig. 55). O'Donoghue & O'Donoghue (1923:163 and 1926).—San Juan Island, Puget Sound. U.W.C.

STIRPARIELLA Harmer 1923. Genotype, *Stirpariella* (*Bicellaria*) *annulata* Maplestone 1879.

Stirpariella occidentalis (Robertson), as *Stirparia occidentalis* in Univ. Calif. Pub. Zool. 2:280, pl. XIII, figs. 72-74, 1905. O'Donoghue & O'Donoghue (1923:164 and 1926).—Puget Sound; Griffin Bay, San Juan Channel off Point Caution, 15-45 meters.

Family FLUSTRIDAE

FLUSTRA Linnaeus 1767. Genotype, *Flustra* (*Eschara*) *foliacea* (Linnaeus) 1758.

Flustra lichenoides Robertson, in Proc. Wash. Acad. Sci. 2:322, pl. XX, figs. 7, 7a, 8, 1900. Robertson (1905:291, pl. XV, figs. 91, 92, and pl. XVI, fig. 105); O'Donoghue & O'Donoghue (1923:165 and 1926).—Channel Rocks, Puget Sound. U.W.C.

MICROPORA Gray 1848. Genotype, *Micropora* (*Flustra*) *coriacea* (Esper) 1791.

Micropora coriacea (Esper), as *Flustra coriacea* in Die Pflanzenthier, pl. VII, fig. 2, 1791. Robertson (1908:275, pl. 17, fig. 26); O'Donoghue & O'Donoghue (1923:172 and 1926).—Griffin Bay, 15-23 meters.

Division COLLOSTEGA Levinsen 1909 (Not known from Puget Sound)

Division PSEUDOSTEGA Levinsen 1909

Family CELLULARIIDAE

CELLULARIA Pallas 1766. Genotype, *Cellularia* (*Eschara*) *fistulosa* Linnaeus 1758.

Cellularia diffusa Robertson, in Univ. Calif. Pub. Zool. 2:289, pl. XV, fig. 90, and pl. XVI, fig. 104, 1905. O'Donoghue & O'Donoghue (1923:165 and 1926).—San Juan Island and Port Orchard Channel, Puget Sound. U.W.C.

Family CRIBRILINIDAE Hincks 1880

PUELLINA Jullien 1886. Genotype, *Puellina* (*Cribrilina*) *gattyae* Busk 1852 and *Puellina* (*Eschara*) *radiata* Moll 1803.

Puellina radiata (Moll), as *Eschara radiata* in Seerinde, p. 63, pl. IV, fig. 17, 1803. Hincks (1884:14); O'Donoghue & O'Donoghue (1923:30 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

REGINELLA?. Genotype, ?.

Reginella furcata (Hincks), as *Cribrilina furcata* in Ann. Mag. Nat. Hist. p. 250, 1882. Hincks (1884:12, pl. XX, fig. 5); O'Donoghue & O'Donoghue (1923:172 and 1926).—Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters.

LYRULA ?. Genotype, ?.

Lyrula hippocrepis (Hincks), as *Cribrilina hippocrepis* in Ann. Mag. Nat. Hist. p. 250, 1882. Hincks (1884:13, pl. XX); Robertson 1908:280, pl. 18, fig. 31); O'Donoghue & O'Donoghue (1923:172 and 1926); as *Lepralia regularis* ibid. (1923:182, pl. III, fig. 27).—Friday Harbor and San Juan Channel, off Point Caution; 40-45 meters.

Family HIPPOTHOIDAE Levinsen 1909

HIPPOTHOA Lamouroux 1821. Genotype, *Hippothoa divaricata* Lamouroux 1821.

Hippothoa divaricata Lamouroux, in Expos. Meth. p. 82, pl. LXXX, figs. 15 and 16, 1821. Robertson (1908:296, pl. 21, figs. 59, 60); O'Donoghue & O'Donoghue (1923:180 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Hippothoa hyalina (Linnaeus), as *Cellepora hyalina* in Syst. Nat. ed. 12, 1767:1286. As *Schizoporella hyalina* Robertson (1903:298, pl. 19, figs. 43-45); O'Donoghue & O'Donoghue (1923:177); as *H. hyalina* ibid. (1926).—Friday Harbor; Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters. Robertson states that it is found from Alaska to California.

Hippothoa hyalina (Linnaeus) var. *incrassata* (O'Donoghue & O'Donoghue), as *Schizoporella hyalina* var. *incrassata* in Contr. Canadian Biol. (1923:177). As *H. hyalina* var. *incrassata* ibid. (1926).—San Juan Channel off Point Caution, 40-45 meters.

Hippothoa hyalina (Linnaeus) var. *intacta* (O'Donoghue & O'Donoghue), as *Schizoporella hyalina* var. *intacta* in Contr. Canadian Biol. (1923:177). As *H. hyalina* var. *intacta* ibid. (1926).—San Juan Channel off Point Caution, 40-45 meters.

Family ESCHARELLIDAE Levinsen 1909

SCHIZOPORELLA Hincks 1880. Genotype, ?.

- Schizoporella crassirostris* Hincks, in Geol. Nat. Hist. Surv. Canada, p. 18, pl. XVIII, fig. 3, 1884. O'Donoghue & O'Donoghue (1923: 178 and 1926).—Friday Harbor.
- Schizoporella cruenta* (Norman), as *Lepralia cruenta* in Ann. Mag. Nat. Hist. 1864. O'Donoghue & O'Donoghue (1926).—San Juan Channel off Point Caution, 40-45 meters.
- Schizoporella dawsoni* Hincks, in Ann. Mag. Nat. Hist. p. 252, 1882. Hincks (1884:20 and as *S. torquata* p. 41, pl. IX, fig. 2); O'Donoghue & O'Donoghue (1926).—San Juan Channel off Point Caution, 40-45 meters.
- Schizoporella insculpta* Hincks, in Ann. Mag. Nat. Hist. p. 252, 1882. Hincks (1884:19, pl. XVII, fig. 5); Robertson (1908:291, pl. 20, figs. 46, 47); O'Donoghue & O'Donoghue (1923:178 and 1926).—Puget Sound, and San Juan Channel off Point Caution, 40-45 meters.
- Schizoporella tumulosa* Hincks, in Ann. Mag. Nat. Hist. p. 252, 1882. Hincks (1884:19, pl. XVIII, fig. 2); O'Donoghue & O'Donoghue (1923:179 and 1926).—Friday Harbor, and San Juan Channel off Point Caution, 40-45 meters.
- Schizoporella umbonata* O'Donoghue & O'Donoghue, in Contr. Canadian Biol. 1926.—San Juan Channel off Point Caution, 40-45 meters.
- SCHIZOPODRELLA Canu & Bassler 1917. Genotype, *Schizopodrella* (*Lepralia*) Johnston 1847.
- Schizopodrella linearis* (Hassall) var. *inarmata* (Hincks), as *Schizoporella linearis* var. *inarmata* in Geol. Nat. Hist. Surv. Canada, p. 41, 1884. Robertson (1908:291, pl. 20, fig. 48); O'Donoghue & O'Donoghue (1923:178 and 1926).—San Juan Channel off Point Caution, 40-45 meters.
- STEPHANOSELLA Canu & Bassler 1917. Genotype, *Stephanosella* (*Lepralia*) (*Eschara*) *biaperta* (Michelin) 1842.
- Stephanosella biaperta* (Michelin), as *Eschara biaperta* in Icon. Zooph. p. 330, pl. LXXIX, fig. 3, 1842. Robertson (1908:287, pl. 19, fig. 41; Hincks (1884:17); O'Donoghue & O'Donoghue (1923:178 and 1926).—San Juan Channel off Point Caution, 40-45 meters.
- SCHIZOMAVELLA Canu & Bassler 1917. Genotype, *Schizomavella* (*Lepralia*) *auriculata* (Hassall) 1842.
- Schizomavella longirostrata* (Hincks), as *Schizoporella longirostrata* in Ann. Mag. Nat. Hist. p. 251, 1882. Hincks (1884:19, pl.

XVII, fig. 4); Robertson (1908:291, pl. 20, fig. 49); O'Donoghue & O'Donoghue (1923:178 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

DAKARIA Jullien 1903. Genotype, *Dakaria chevreuxi* Jullien 1903.

Dakaria ordinata (O'Donoghue & O'Donoghue), as *Schizoporella ordinata* in Contr. Canadian Biol. p. 180, pl. III, fig. 25, 1923. Ibid. (1926).—San Juan Channel off Point Caution, 40-45 meters.

LEPRALIA Johnston 1847. Genotype, ?.

Lepralia columbiae O'Donoghue & O'Donoghue, in Contr. Canadian Biol. 1926.—San Juan Channel off Point Caution, 40-45 meters.

Family STOMACHETOSELLIDAE Canu & Bassler 1917

STOMACHETOSELLA Canu & Bassler 1917. Genotype, *Stomachetosella crassicolis* Canu & Bassler 1917.

Stomachetosella sinuosa (Rusck), as *Lepralia sinuosa* in Quart. Jour. Mic. Sci. VIII:125, pl. XXIV, figs. 2 and 3, 1860. O'Donoghue & O'Donoghue (1923:177 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Group MICROPORELLAE Canu & Bassler 1917

FENESTRULINA Jullien 1888. Genotype, *Fenestrulina (Cellepora) Malusii* Savigny-Audouin 1826.

Fenestrulina malusii (Savigny-Audouin), var. *umbonata*, as *Cellepora malusii* in Audouin Explic. Savigny Egypte, p. 239, pl. VIII, fig. 8, 1826. Hincks (1884:16); Robertson (1908:282, pl. 18, figs. 35, 36); O'Donoghue & O'Donoghue (1923:174 and 1926).—U. W.C., and San Juan Channel off Point Caution, 40-45 meters.

MICROPORELLA Hincks 1877. Genotype, *Microporella (Eschara) ciliata* (Pallas) 1766.

Microporella californica Hincks, as *M. ciliata* form *californica* in Geol. Nat. Hist. Surv. Canada, p. 16, pl. XVII, fig. 3, 1884. Robertson (1908:281, pl. 18, figs. 32-34); O'Donoghue & O'Donoghue (1923:174 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Microporella ciliata (Pallas), as *Eschara ciliata* in Elench. p. 38, 1766. Hincks (1884:14); O'Donoghue & O'Donoghue (1923:173 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

M. ciliata var. *umbonata* Hincks, in Geol. Nat. Hist. Surv. Canada, p. 15, pl. XVII, fig. 1, 1884. O'Donoghue & O'Donoghue (1923:173 and 1926).—Friday Harbor; Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters.

M. ciliata var. *vibraculifera* Hincks, in Geol. Nat. Hist. Surv. Canada 1884:15, pl. XVII, fig. 2. O'Donoghue & O'Donoghue (1923: 173 and 1926).—Friday Harbor; Griffin Bay, and San Juan Channel off Point Caution, 40-45 meters. U.W.C.

Family EURYSTOMELLIDÆ Levinsen 1909

EURYSTOMELLA Levinsen 1909. Genotype, *Eurystomella* (*Lepralia*) *foraminigera* (Hincks) 1883.

Eurystomella bilabiata (Hincks), as *Lepralia bilabiata* in Ann. Mag. Nat. Hist. p. 49, pl. 3, figs. 1, 1a, 1b, 1884. Robertson (1908: 298, pl. 21, figs. 61-64); O'Donoghue & O'Donoghue (1926).—Puget Sound. U.W.C.

Family SMITTINIDÆ Levinsen 1909

SMITTINA Norman 1903. Genotype, *Smittina* (*Lepralia*) *reticulata* MacGillivray 1842.

Smittina cellata (O'Donoghue & O'Donoghue), as *Smittia cellata* in Contr. Canadian Biol. p. 185, pl. IV, fig. 31, 1923. Ibid. (1926).—San Juan Channel off Point Caution, 40-45 meters.

Smittina collifera (Robertson), as *Smittia collifera* in Univ. Calif. Pub. Zool. p. 304, pl. 23, figs. 72 and 73, 1908. O'Donoghue & O'Donoghue (1923:185 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Smittina columbiana (O'Donoghue & O'Donoghue) as *Porella columbiana* p. 183, pl. III, fig. 28, 1923. Ibid. (1926).—Friday Harbor.

Smittina concinna (Busk), as *Porella concinna* in Brit. Mus. Catalog. 2:67, pl. XCIX, 1854. Robertson (1908:300, pl. 22, fig. 65); O'Donoghue & O'Donoghue (1923:182 and 1926).—San Juan Channel off Point Caution, 40-45 meters.

Smittina landsborovii (Johnston), as *Smittia landsborovii* in Brit. Zooph. ed. 2, p. 310, pl. LIV, fig. 9, 1847. Robertson (1908:305, pl. 23, fig. 74); O'Donoghue & O'Donoghue (1923:184 and 1926).—Friday Harbor; Griffin Bay, and San Juan Channel off Point Caution, 40-45 meters.

Smittina marsupium (MacGillivray), as *Lepralia marsupium* in Descr. Australian Polyzoa, 1868. Hincks (1884:24, pl. IV, fig. 4); O'Donoghue & O'Donoghue (1923:182 and 1926).—Friday Harbor; Griffin Bay, and San Juan Channel off Point Caution, 40-45 meters. U.W.C.

Smittina torquata (O'Donoghue & O'Donoghue), as *Smittia torquata* in Contr. Canadian Biol. (1923:185, pl. IV, fig. 32). Ibid. (1926).—San Juan Channel off Point Caution, 40-45 meters.

- Smittina trispinosa* (Johnston), as *Smittia trispinosa* in Edin. Phil. Jour. p. 322, 1838. Robertson (1908:302, pl. 22, figs. 68-70); O'Donoghue & O'Donoghue (1923:185 and 1926).—Friday Harbor, and San Juan Channel off Point Caution, 40-45 meters. U.W.C. Robertson states that it is found from Alaska to San Diego.
- MUCRONELLA Hincks 1880. Genotype, *Mucronella (Lepralia) peachii* (Johnston) 1847.
- Mucronella peachii* (Johnston), as *Lepralia peachii* in Brit. Zool. ed. 2, p. 315, pl. LV, figs. 5 and 6, 1847. O'Donoghue & O'Donoghue (1923:187 and 1926).—Friday Harbor; Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters.
- Mucronella pavonella* (Alder), as *Eschara pavonella* in Quart. Jour. Micro. Sci. n. s. IV:12, 1864. Hincks (1884:26); Robertson (1908:308, pl. 23, figs. 78, 79); O'Donoghue & O'Donoghue (1923:188 and 1926).—San Juan. U.W.C.
- Mucronella simplicissima* Busk var. *perforata* O'Donoghue & O'Donoghue, in Contr. Canadian Biol. (1923:188). Ibid. (1926).—San Juan Channel off Point Caution, 40-45 meters.
- Mucronella ventricosa* (Hassall), as *Lepralia ventricosa* in Ann. Mag. Nat. Hist. IX:412, 1841. Hincks (1884:26); O'Donoghue & O'Donoghue (1923:188 and 1926).—San Juan Channel off Point Caution, 40-45 meters.
- RHAMPHOSTOMELLA Lorenz 1886. Genotype, *Rhamphostemella costata* Lorenz 1886.
- Rhamphostomella costata* Lorenz, in Bryozoen von Jan Mayen, Die Oesterreichische Polar Station Jan Mayen 3:11, 1886. O'Donoghue & O'Donoghue (1923:186 and 1926).—San Juan Channel off Point Caution, 40-45 meters.
- PORELLA Gray 1848. Genotype, *Porella (Millepora) cervicornis* Pallas 1766.
- Porella bispina* O'Donoghue & O'Donoghue, in Contr. Canadian Biol. p. 183, pl. III, fig. 29, 1923. Ibid. (1926).—Griffin Bay, and San Juan Channel of Point Caution, 15-45 meters.
- Porella cribriformis* O'Donoghue & O'Donoghue, in Contr. Canadian Biol. p. 184, pl. IV, fig. 30, 1923. Ibid. (1926).—Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters.
- Porella major* Hincks, in Geol. Nat. Hist. Surv. Canada p. 25, pl. IV, fig. 5, 1884. O'Donoghue & O'Donoghue (1923:183 and 1926).—Griffin Bay, and San Juan Channel off Point Caution, 15-45 meters.

Family RETEPORIDAE Smitt 1867

PHIDOLOPORA Gabb & Horn 1862. Genotype, *Phidolopora* (*Retepora*) *labiata* Gabb & Horn 1862.

Phidolopora pacifica (Roberston), as *Retepora pacifica* in Univ. Calif. Pub. Zool. p. 310, pl. 24, figs. 81-84, 1908. O'Donoghue & O'Donoghue (1923:189 and 1926).—Puget Sound and Griffin Bay, 15-45 meters.

Family PHYLACTELLIDAE Canu & Bassler 1917

PHYLACTELLA Hincks 1879. Genotype, *Phylactella* (*Lepralia*) *labiosa* (Busk) 1852.

Phylactella pacifica O'Donoghue & O'Donoghue, in Contr. Canadian Biol. p. 186, pl. IV, fig. 33, 1923. Ibid. (1926).—Friday Harbor, and San Juan Channel off Point Caution, 40-45 meters.

LAGENIPORA Hincks 1877. Genotype, *Lagenipora socialis* Hincks 1877.

Lagenipora erecta O'Donoghue & O'Donoghue in Contr. Canadian Biol. p. 175, pl. III, fig. 22, 1923. Ibid. (1925).—U.W.C.

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Sub-order ASCOPHORA (Not known from Puget Sound)

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Anatomy of the Millipede *Chonaphe Armatus*

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Morphologically the Myriapoda of the United States have been somewhat neglected. Wood (1865), Harger (1872), Cook (1896) and Broleman (1922) have accomplished much of taxonomic value but have largely omitted reference to the morphology of the group. These facts seem to justify submission of the results of studies made upon the morphology of *Chonaphe armatus* (Harger) Cook, a western millipede. In 1872 Harger described this form as *Polydesmus armatus*, but in 1893 Bollman renamed the species *Leptodesmus armatus*. Bollman's work however has been superseded and the species has been placed in the genus *Chonaphe* by Cook (1904) whose classification for this species follows.

"Order MEROCHAETA—Diplopoda with 19 or 20 segments, the superficial hardened parts of which are coalesced into complete rings. Eyes are wanting in all members of this order, which never-the-less contains a large proportion of the brightly colored species of the Diplopoda. Nearly all the Merochaeta have distinct lateral carinae or projections from the segments, on which are located the repugnatorial pores or openings of glands, which, in the members of this order, secrete prussic acid. It is also characteristic that the pores, which begin on segment 5, are not found on all the other segments, but are always absent at least from segment 6, and usually from several others. The normal or most general pore formula, that which prevails on all the species described below, is 5. 7, 9, 10, 12, 13, 15, 16, 17, 18, and 19.

"Family CIELODESMIDAE—Body moniliform, the carinae distinctly separate; claws slightly and evenly curved. Repugnatorial pores laterally located in small depressions of the thickened margins of the carinae; dorsal surface evenly convex, smooth.

"As at present constituted, this family extends throughout tropical and temperate America, where it is richly represented in genera and species. A few Asiatic species described under *Oxyurus* also probably belong to the same series, which is at present defined by negative rather than by positive characters. The characters given in the following key apply to all the species in the United States, but the alliances of many tropical types are still very uncertain.

"Genus CHONAPHE—Gonopods very long, the anterior branch large and complex, with thin crests and plates; antennae longer than width of body.

"Type *Chonaphe armatus*—Body rather small and slender; dorsum moderately convex; carinae inserted higher up and less thickened on the margin than in related western genera. Antennae filiform, longer than the body is wide; legs also long and slender in comparison with those of related genera. Gonopods much longer than in allied forms, the laminate cristate anterior branch much longer than the slender and strongly incurved posterior branch."

The material used in these studies was collected in the Puget Sound region of the State of Washington and represents such widely separated points as Seattle, Beef Harbor in Kitsap County, the San Juan Islands, and even the slopes of Mount Baker. The species had been reported only from the eastern part of Washington and from the region of the John Day river in Oregon.

It is impossible to give specific references for the nomenclature herein used because it has seemed more desirable to adopt portions of the nomenclatures of Packard (1873), Cook (1896) and Verhoeff (1902) than to follow that of any one author exclusively.

The writer wishes to acknowledge the assistance of Dr. Horace Gunthorp who is responsible for the identification of the species. Acknowledgment is also due Professor Trevor Kincaid, Dr. J. E. Guberlet and Dr. E. Victor Smith for their valuable suggestions during the preparation of the manuscript.

EXTERNAL ANATOMY

The body is slender and consists of from 18 to 20 segments. In this respect it does not agree with Cook's description, which calls for 19 or 20 segments. The variation naturally affects Cook's pore formula.

In most cases the color of the living animal is jet black but at times an individual is found which shows a purple tinge. Preservation in either alcohol or formalin tends to bleach the material to a chestnut brown or olivaceous color. The descriptions of Harger (1872) and Wood (1865) were based upon study of preserved material. The carinae, the basal segments of the antennae, the inferior border of the face and in some cases the anal scuta are lemon yellow.

A transverse groove separates each segment into two nearly equal parts. The anterior portion tapers slightly and is inserted into the flared posterior division of the segment in front. The posterior half bears typically two pairs of appendages. This half is again divided by a second faint transverse line, which separates the pairs of appendages one from the other. Lateral extensions of the scuta are known as carinae. The thickened margins of these carinae are indented to form cup-like depressions in which are located the repugnatorial pores. Pores do not occur on every segment as has been previously noted. Segments 1, 2, 3, 4, 6, 8, 11, 14 and the terminal one bear no pores.

The head is formed mainly of the part designated as the epicranium, which may be incorrectly named, for it seems to have no true homology with the clypeus of the Hexapoda. Just anterior to the an-

tennae is a short broad region slightly set off from the epicranium by a faint groove. This is often referred to as a pseudoclypeus. The antero-median margin of the pseudoclypeus is broadly emarginate; the edge is lined with sturdy bristles. Just under the edge of this pseudoclypeal region is the point of attachment of the labrum. The latter structure extends downward and fills in the indentation of the pseudoclypeus.

The labrum is a broad plate which forms the ventral half of the anterior aspect of the head. Its ventral margin is deeply notched and the margins of the notch are extended to form three large teeth. Like the pseudoclypeus, the labrum bears an hirsute covering. It is due to the coloration of the labrum that the inferior border of the face exhibits the lemon color already noted. An internal extension of the labrum projects backward into the buccal cavity and forms the roof of that region. Many of the mouth muscles have their attachment on the walls of the pocket formed between this extension and the pseudoclypeus.

The antennae arise close together on the anterior aspect of the head. Their basal segments articulate with very short and pliable extensions of the exoskeleton, which have their origin at the bottom of shallow pits located just in front of the dorso-lateral angle of the head. In a state of rest the first segment occupies a groove, which extends outward and upward over the head. The first five segments are broad distally and taper toward their proximal ends. The sixth or terminal segment is short and bud-like. Its tip is deeply indented and bears four conical spikes within the depression. During periods of activity the antennae are extended in front of the moving animal and serve as tactile organs. The surface of the antenna is covered with long spiny hairs which are more densely placed on the distal segments. The growth on the basal segments is stocky and more spike-like.

The antennae are moved by means of a system of muscle strands running diagonally between adjacent segments.

Packard (1873) is of the opinion that the gnathochilarium, because of its embryological relations, should be considered as the homologue of the first maxillae of the insects. Recent workers (Verhoeff and others) are agreed in their opinion that the gnathochilarium should be recognized as the result of fusion of the first maxillae. In *Chonaphe armatus* this structure consists of four main divisions: (a) a partially chitinized inner lamella-like plate designated as the tongue lobe; a compound outer plate composed of (b) a pair of lateral plates called

the stipites gnathochilarii, and (c) another pair of median plates called the lamellae lingualis; (d) a posterior plate called the duplomentum.

The tongue lobe (Fig. 3 TL) is attached to the inner surfaces of the lamellae lingualis and extends a short distance beyond their anterior margins. It is medially cleft; the points so formed are slightly pitted and bear from one to three short spines. These pitted points (Fig. 3 LI) are the lobi interior.

The stipites gnathochilarii are two elongated plates (Fig. 3 SG), which form the lateral margin of the gnathochilarium. The median anterior angle of each stipite bears a pair of movable finger-like projections. Their tips are slightly pitted and the pits bordered by seven short sturdy spines. These projections (Fig. 3 LE, LM) are designated as the lobi exterior and medius respectively. Verhoeff (1902) supposes them to be organs of taste. The anterior surfaces of the stipites are covered with numerous long, slender, curved spines. Along the medial margins these are replaced with shorter spines more thickly set. The stipites are continued anteriorly as very thin plates occupying a position dorsal to the lobi exterior and medius. The margins of these plates are densely fringed with slender curving filaments.

The lamellae lingualis (Fig. 3 LL) are much like the stipites in general outline but are greatly reduced in size. The anterior margins are comparatively smooth and bear no processes. The anterior surfaces, like those of the stipites, are covered with slender spines which continue posteriorly along the lateral margins but become reduced in size toward the posterior angles.

The labiella, or "Zentralkörper" of Verhoeff, apparently has its origin in the same region as that of the tongue lobe. It seems to be derived from the lamellae lingualis for there are two diverging posterior extensions of the labiella, which ultimately become merged with these structures. Packard names these the stiles. The labiella lies between the lamellae and the tongue lobe and partially covers the cleft in the latter.

In the angle formed by the union of the lamellae and the stipites is to be found the large triangular duplomentum (Fig. 3 D), which appears to be the product of fusion of the mentum and promentum of Verhoeff. The duplomentum is covered with short spines which become smaller and more dense toward the anterior margins.

Posterior to the gnathochilarium is a slender curved plate, the gula. The posterior margin is concave to provide for ventral flexure of the head. The space between the curved margin of the gula and

the anterior margin of the second body segment is covered with a semi-chitinous membrane.

The first body segment is incomplete; it is only the dorsal arch or scuta of a normal segment and bears no appendages. The second segment is small but complete and bears a single pair of legs, which extends forward beneath the gnathochilarium. The third segment of the male is normal. The scuta and sterna are fused to form a solid ring and there are two pairs of walking legs. In the female the third segment is abnormal. It gives rise to a normal pair of walking legs but the sterna are incompletely fused posteriorly and form an oval opening in the exoskeleton from which emerge the pair of female genitalia. Bröleman and Lichtenstein (1919) advance the view that these are merely chitinized extensions of the membrane about the apertures of the oviducts. Verhoeff (1902) believes that they should be considered as modified legs. Bröleman (1922) criticises Verhoeff's evidence and suggests that Verhoeff has perhaps been somewhat dogmatic in his statements. The fourth, fifth and sixth segments are normal in both male and female. The seventh segment in the male gives rise to the single pair of male genitalia. They too emerge from an opening in the sterna of the segment just as do those of the female. To the writer these appendages much more clearly suggest modification of typical legs than do the vulvae of the female. A careful embryological study should clear up the question of their origin.

With the exception of the two terminal segments all other segments of both sexes are normal. The last two segments bear no appendages. The penultimate segment is perfectly formed but is much shortened. The last segment is greatly modified. The dorsum is drawn out into a subtriangular anal scute and the ventral portion is shortened. Ventrally a hemispherical plate articulates with the last segment in such a manner that its free margin may move dorsad toward the anal scute. The large anal aperture is closed by two spherical sectors, whose median margins closely articulate when apposed. These plates rotate on dorso-ventral axes. The rectum is attached to the median margins of these plates, and when the animal is anaesthetized or mechanically stimulated the plates separate and partially evert the rectum. The writer has never observed normal evacuation and so is unable to say that the same conditions exist at such times.

The typical walking leg consists of five segments and a large terminal claw or hook. The leg arises from a heavy basal stock, which is fused to the sterna and basal stocks of the other legs of the segment. The first four segments of the leg resemble those of the an-

tennae in shape but are not so uniform in size. The first two segments are nearly equal in size and are cylindrical in shape. The third and fourth segments are shorter and more rotund than are the other segments of the leg. The terminal segment is long and slender and tapers slightly toward the distal end. The claw is long and curved. Each segment is covered more or less densely with hairy bristles. The leg is moved by groups of muscles lining the exoskeleton. These muscles are intersegmental and serve to extend and flex the various segments. There is some movement in a vertical plane but the articulation of the segments is such that a large part of the movement is parallel to the main axis of the body. Mechanical stimuli demonstrate that there is power to move each leg independently but locomotion is rhythmic and proceeds from anterior to posterior.

The female copulatory organs or vulvae are capable of being withdrawn within the body and are so found in a condition of rest. There are certain external stimuli which cause the female to extend the vulvae but the writer is not familiar with the nature of the stimulation.

The vulva itself is formed of two parts, which are loosely connected and moveable one on the other. The proximal division resembles an inverted truncated cone the base of which has been slightly compressed so that its long axis is at right angles to the long axis of the body. The external or distal portion is somewhat kidney-shaped with the concave surface pressed firmly against the flattened base of the basal part. The entire organ has a compressed appearance in a transverse plane. The terminal division is so tilted as to bring the median end well above the remainder of the structure. Bröleman gives these two divisions of the vulva the names of "mound" (Fig. 7 SN) and "shield" (Fig. 7 S). The shield is made up of two plates closely articulating along their ventral margins and resembling a bivalve shell; hence the name "valve" suggested by Bröleman for these plates.

The "oviductal aperture" of Bröleman (Fig. 7 OA) is located in the median end of the shield close to the point of articulation with the mound. The aperture is funnel-shaped and is formed by an invagination of the exoskeleton. The oviduct joins the inner end of the funnel.

The surface of the vulva is protected by closely set bristles, which are most prominent along the groove marking the articulation of the two valves of the shield.

It has been thought advisable to use Harger's (1872) description

of the gonopods. This description appears under the name *Polydesmus armatus* as noted.

"The large male appendages are hairy at their base and consist of two principal portions; the larger and inner is cylindrical for the first third of its course and directed downward, inward and forward; it then becomes lamelliform, and sends inward and upward a much excavated process (Fig. 8 EP1), distally a smaller and less excavated one (Fig. 8 EP2), and is at this point contracted but expands so as to terminate in a much bent plate. The other portion is a long curved spine (Fig. 8 CS) on a bristly cylindrical base, arising a little behind and outside the former and curving spirally around it so that its attenuated tip is received in the excavated process. A small stout hooked spine is nearly concealed by the bristles that spring from the base of the larger spine." Harger's description is essentially correct though in some minor points it fails to agree with the material from the Puget Sound region. This may be due to regional variation.

INTERNAL ANATOMY

The interior of the exoskeleton is lined with a loose network of muscle bundles, which flex the body segments and move the legs. Within this loose muscular structure is a tough connective tissue layer which constitutes the body wall. The coelomic space, enclosed by this wall, contains the usual organs to be found within the body of a millipede.

In the male specimen the intestinal tract completely fills the body cavity. It is almost impossible to separate the tract because of its close relation to the wall. The same condition prevails in the female during the resting period, but as the ovaries ripen the egg mass occupies more and more space until it has entirely surrounded the alimentary canal and filled the coelom.

Just within the margins of the mouth are the mandibles. The anterior end of each mandible is drawn out into a long curved hook or tooth directed forward and medialward. Formed from the same chitinous plate but posterior to this hook is a smaller rasping tooth followed in turn by a series of rounded cutting teeth (Fig. 6 CT). These hooks and cutting edges are used to shred and reduce the decaying vegetable matter which forms the principal diet of this animal. Behind the above described structures is a dome-shaped plate whose surface is thrown into transverse ridges which are surmounted by delicate hairs all trained toward the oesophagus. A second plate (Fig. 6 CP) projects inward. This plate is heavily chitinized and its surface is

also thrown into transverse ridges the summits of which are finely corrugated. A soft fleshy apron (Fig. 6 A) with coarsely fringed margins is attached to the base of the mandible and extends medialward in a horizontal plane. The jaws are moved by a powerful set of muscles which have their point of attachment in the roof and lateral chambers of the buccal cavity.

Far back in the buccal cavity and in front of the oesophageal aperture is a chitinous rod consisting of two curved members which extend in from the side walls of the buccal cavity, and a third connecting cross-member. In the center of the cross-member is a short thick extension of the chitinous structure, which is directed backward toward a pair of jaws of very light construction. The jaws and a delicate membrane which extends inward from the buccal walls, are supported by the curved rod before described. Muscles from the buccal walls operate the jaws. Other muscles appear to be capable of lifting the rod structure in such a manner that the centrally located extension acts as a feeder for the jaws. The membrane serves to direct the finer particles of food through the jaws. The author has failed to find any reference to this structure (Fig. 5) in the literature and proposes the name accessory buccal apparatus for the structure.

One other feature of the cephalic region deserves mention. Here are to be found several structures which other workers have described as glands. In the upper part of the head there is a large irregular mass which Reinecke (1910) has named the posterior salivary gland. A similar mass of glandular tissue, which he calls the head gland or anterior salivary gland, is located in the labral region. Between the lamellae lingualis and the tongue lobes of the gnathochilarium there are several small masses of such tissue, described by Verhoeff as salivary glands. A structure resembling the tubular gland described by Krug (1906) was observed following the line of the stomach and oesophagus forward.

The oesophagus is the smallest of the divisions of the digestive system, occupying as it does only the head region and the first body segment. It is of very small diameter but has muscular walls of considerable thickness. The cephalic and caudal portions of the oesophagus have a tubular lumen free of all obstructions. The central part however possesses a lumen that is star-shaped in cross-section. This effect is produced by the six longitudinal ridges thrown up on the walls of the oesophagus. Krug (1906) sees a similarity between these six folds and the Kaumagen or proventriculi of the insects.

Nearly two-thirds of the alimentary canal is set apart as a stomach. In structure it is of the greatest simplicity; it is a straight tubu-

lar structure with muscular walls lined with a somewhat spongy glandular tissue. Near the anterior end is the straight tubular gland which Krug indicates as one secreting digestive fluids. Between stomach and foregut is an effective sphincter.

Greater complexity is exhibited in the organization of the intestine than in the other parts discussed. Midway in its length is a pronounced constriction which is the seat of a lesser sphincter. The anterior half of the gut shows little difference in structure from the stomach. The most important feature of this region is the presence of the Malpighian tubes, a pair of glands described by other workers as excretory because of their rectal position. These tubes which lie one on either side of the intestine are straight or simply coiled and empty into the tract at a point just in front of the second sphincter. Because of their peculiar position with reference to the digestive tract the author is inclined to raise a question as to their real function and wishes to suggest that they may be of aid in digestion.

The post-intestine is comparatively thin walled. Multitudinous folds in the walls provide for considerable expansion in this hinder portion. An anal sphincter closes the hindgut to the rectal chamber. As previously noted the posterior margins of the rectal chamber are attached to the median edges of the anal plates and so may be everted.

The female reproductive system consists of a single ovarian mass and a common oviduct, which sends a branch to each vulva. Some authors are convinced that the ovarian mass is in reality two ovaries; others hold to the view that but one may be demonstrated. The writer is convinced that there is in *Chonaphe armatus* but one ovarian sack, which encloses two germ tracts. This compound structure extends nearly the entire length of the coelomic space. As the eggs mature the two germ tracts are obliterated and the ovarian structure seems to be one. Each egg is supported within a delicate sac-like membrane which is joined to similar sacs to form a racemose structure. In one specimen two parallel convoluted tubes were observed to lie along the ventral side of the egg mass in a position corresponding to the original germ tracts. Unfortunately the specimen was so badly damaged that it was impossible to trace their course forward with any degree of certainty. They appeared however to continue cephalad until they met in the region of the oviduct.

The ovarian sack terminates abruptly in the common oviduct, which is short, thick walled and rather broad. The two anterior branches of the latter curve to either side early in their course. After making a partial turn upon themselves they enter the mounds of the respective vulvae. The oviduct keeps well to the outer or lateral wall

ot the mound and enters the shield at the outer margin. It then follows the contour of this structure almost to the oviductal aperture. It makes a broad loop upon itself before entering the aperture.

In general, the male organs of reproduction resemble those of the female. There is a common testicular sack which encloses two slender germ tracts. A common vas deferens branches, one branch going to each gonopod. Transference of spermatozoa from the male to the vulvae of the female takes place through minute grooves which extend the length of the male copulatory organs.

Like that of all arthropods, the nervous system of *Chonaphe armatus* is simple in organization. It consists of a bilobed brain situated over the buccal end of the oesophagus, circumoesophageal connectives meeting ventrally in a suboesophageal ganglion and a ventral nerve cord. The cord gives rise, in each segment, to a large ganglionic mass which previous workers have stated to be a compound ganglion produced at the time of segmental union. The mass is large anteriorly but tapers to the posterior limits of the segment. It gives rise to four pairs of lateral nerves. Branches extend to the alimentary canal, the legs, the muscles of the trunk and to the digestive system. Some authors have called attention to a slight constriction in the ganglionic mass, which they contend marks the fusion of two ganglia. Delicate nerves arise in the dorsal brain mass to supply the cephalic regions.

The respiratory system may be dismissed with the statement that there are two simply coiled, unbranched tracheae in each segment, as is typical of the diplopoda.

SUMMARY

1. A somewhat detailed morphological study of the millipede *Chonaphe armatus* (Harger) Cook is here reported.
2. An hitherto undescribed buccal structure is noted for which the author suggests the name accessory buccal apparatus.
3. Additional notes on the distribution of *Chonaphe armatus* indicate that its range is wider than has been supposed.

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PLATE 5

All figures were made with the aid of a camera lucida.

A, apron	LE, lobus exterior
CP, corrugated plate	LI, lobus interior
CT, cutting teeth	LL, lamella lingualis
D, duplomcntum	LM, lobus medius
F, feeder	R, rod
I, jaw	SG, stipites gnathochilarium
L, labiella (Zentralkörper)	TL, tongue lobe

FIG. 1. Labrum of *Chonaphe armatus*. $\times 15$.

FIG. 2. Antenna. $\times 18$

FIG. 3. Gnathochilarium. $\times 26$.

FIG. 4. Walking leg. $\times 15$.

FIG. 5. Accessory buccal apparatus. $\times 15$.

FIG. 6. Mandible. $\times 21$.

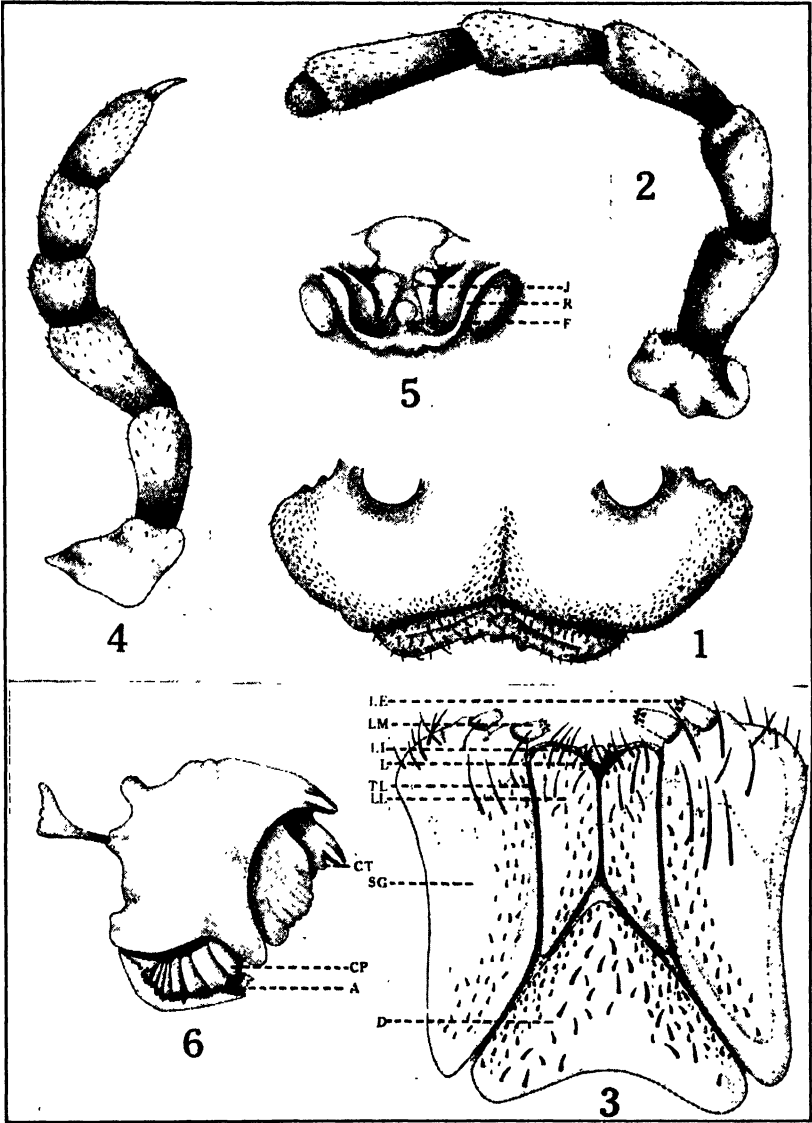


PLATE 5

PLATE 6

Figure 14 is a freehand drawing; the others were made with the aid of a camera lucida.

AN, anus	Mu, mucosa
B, brain	O, oviduct
CC, circumoesophageal connective	OA, oviductal aperture
CE, columnar epithelium	Oes, oesophagus
CS, curved spine	PI, post-intestine
EP1, large excavated process	S, shield
EP2, small excavated process	SN, mound
MC, circular muscle	SoG, suboesophageal ganglion
MG, midgut	St, stomach
ML, longitudinal muscle	VN, ventral nerve cord
MpT, Malpighian tube	

FIG. 7. Vulva. $\times 33$.

FIG. 8. Gonopod. $\times 33$.

FIG. 9. Digestive tract.

FIG. 10. Cross section of oesophagus. $\times 20$.

FIG. 11. Cross section of stomach. $\times 20$.

FIG. 12. Cross section of midgut. $\times 20$.

FIG. 13. Cross section of post-intestine. $\times 20$.

FIG. 14. Nervous system. $\times 21$.

FIG. 15. Trachea.

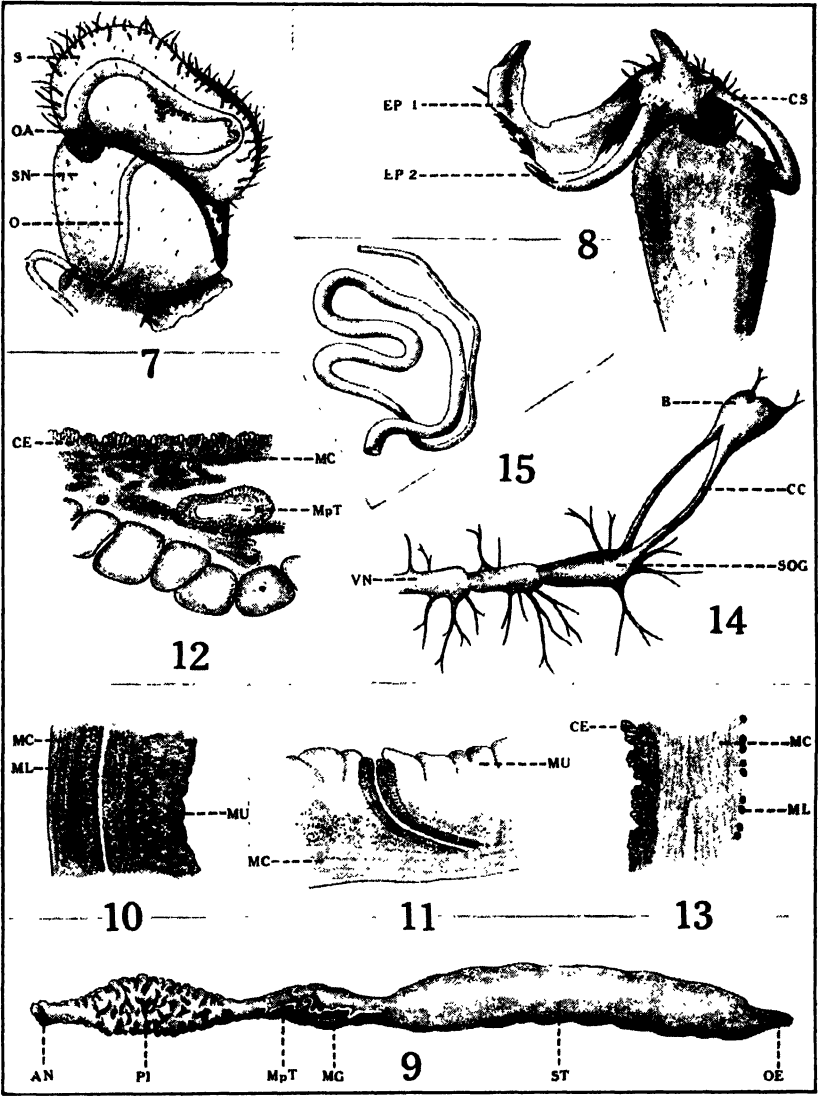


PLATE 6

Some Steps in the Development of *Porphyra Naiadum*

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MORPHOLOGY

Porphyrum naiadum Anderson is a red alga of the Bangiaceae which grows on *Zostera marina* and *Phyllospadix scouleri*. It has a cushion-shaped base from which grow monostromatic fronds. The fronds are oblanceolate, wine red to blue-purple, 2-10 cm long, .025-.030 mm thick. The cells of the fronds are nearly square as viewed from the surface, .015-.020 mm in diameter, with little jelly between them. The surface jelly measures about .005 mm.

It is the only species of *Porphyra* to have the cushion-shaped base, all other species having a disk made up of rhizoid-like or hypha-like outgrowths from the lower cells of the frond.

The object of this paper was to investigate this cushion type of base and the development of the frond from it. At the same time an attempt was made to determine why it grows only on the two host plants mentioned and why it is confined to the edges of these.

The plants used were growing on *Zostera* on the south side of Brown Island and on *Phyllospadix* at False Bay, all in the vicinity of the Puget Sound Biological Station. All the sections used were cut free hand from fresh material. By stripping off the outer edge of the eel grass and examining under the microscope the young stages could easily be found and examined.

A gelatinous sheath surrounds the mass of cells in the early stages and probably serves as a method of attachment to the host plant as no other means could be found. The short rhizoidal outgrowths mentioned by Hus¹ were not observed in these stages but were found in the late summer cushions. The very young and even mature plants were easily detached from the host.

A spore settles down on *Zostera* or *Phyllospadix*, apparently attaching itself by a thick gelatinous sheath which forms around it (Fig. 2). This by successive divisions, at first in one plane, each division at right angles to the one before, forms a little plate on the edge of the eel grass (Figs. 3, 5, 6, 7, 8, 10, 11, 13, 14). Later by subdividing in two planes they become several layers in thickness and form the cushion-shaped base (Figs. 15, 16). These divisions can be

¹ Hus, Henri T. A., "An account of the species of *Porphyra* found on the Pacific Coast of North America." Proc. Calif. Acad. Sci. 2:No. 6.

followed until over a hundred cells have been produced when the body becomes too large and thick to be examined under the high power of the microscope. The central cells soon become much larger than those at the edge, apparently because the latter divide more frequently (Figs. 13, 14). The center of the cushion is the thickest portion, thus giving the body a hemispherical shape in cross-section (Figs. 15, 16, 19).

In this paper the word frond is used to denote the flat leaf-like part of the plant and the word cushion the thick basal portion. The formation of the frond usually begins as a ridge of central cells, although Hus says that any cell of the base seems to be capable of beginning the formation of the frond. It is always formed from the outer layer of cushion cells (Fig. 25). Often many of the cushions grow so crowded together on the blade of *Zostera* that they become indistinguishable from one another, and form a rather flat solid covering over the edge of the eel grass (Fig. 34). At other times large rounded, much lobed, cushions are formed crowded together on the edge of the blade of *Zostera* (Fig. 31). Many fronds are produced from these bases. As many as two dozen may be produced within the length of an inch of the *Zostera* edge. Sometimes however, blades of *Zostera* are found with the edges crowded with cushions and but few fronds coming from them. Cushions over .5 cm high have also been found with no fronds whatever. The cushions commonly do not reach that size but average about 1-2 mm in height.

The fronds start forming when the base is very small, the cushion then grows larger with the growth of the frond, and eventually forms a sort of cup about its base (Fig. 24).

In cross-section these cushion-like bases were found to be made up of a compact outside layer of cells resembling somewhat those of the frond in size and contents. The layer of cells next the eel grass was very much like the outer layer but the chloroplast was somewhat smaller. The interior cells were large thin walled and easily crushed, and there were large intercellular spaces. The chloroplast was very much reduced or entirely absent in the interior cells, probably through lack of light and activity of the cells (Fig. 27). No method of attachment could be made out in any of the bases other than that the cushion overlapped the edge and was closely appressed to both sides of the blade.

The work was begun in June, and in August a different type of the cushion-like base was found on the eel grass. Rough irregular patches were found all over the blade and not alone on the edges. These were a few layers thick and appeared as though formed from

many spores rather than by the successive divisions of one spore. Nearly all the fronds were forming spores at this time. The fruiting patches were formed at the tip; this became detached from the rest of the frond and floated away as a thin film of spores. These films stick to anything with which they come in contact. It may be that the cushions found on the eel grass in August were due to groups of these spores lodging in one place and all beginning growth there so that they formed the irregular masses mentioned above (Figs. 20 and 21). The inner layers of cells were larger, as before. The layers next the eel grass had rhizoid-like outgrowths extending through the thick layer of jelly (Fig. 28). Hus reports these cushion-like patches covering the blades of the eel grass as the winter form of *Porphyra naiadum*.

ATTEMPTS AT CULTIVATION

Many attempts were made to grow the spores in the laboratory without much success. Other species of *Porphyra* have been grown but so far as could be determined *Porphyra naiadum* had never been tried. Fruiting material was collected and the spores placed in dishes which were kept in running water to insure a low temperature. This water however, often became quite warm on hot days. Both filtered and boiled sea water, also sea water with CaCl_2 , NaNO_3 and CaHPO_4 added were used as culture solutions. All the spores thus planted in June and early July disintegrated within two or three days. The juice of *Zostera* was added to water in which spores were planted, on the supposition that *Porphyra* might be partially parasitic upon *Zostera*; this also failed. The rapid disintegration of the spores at this time may have been due to the hot weather during that period. On July 15th more spores were planted in the different culture solutions mentioned above. Three weeks later some of the spores were still alive or at least had not disintegrated as the former ones had done. At the end of two weeks a few of these had divided once but made no further growth. Covering the culture dishes with colored paper to keep down the amount of light seemed to make no difference. Attempts were made to get spores to grow on different green algae and on rocks, but these failed.

Bubbles were often seen issuing from the edges of the eel grass. The gases liberated here suggested a possible reason for the *Porphyra* growing on the edge of the blade only. An apparatus was set up to aerate the water. Three different plantings of spores lived less than a week each time, and then disintegrated as before. They made no growth.

That *Porphyra naiadum* was restricted to *Zostera* and *Phyllospadix*, the only flowering plants growing submerged in salt water. suggested that the *Porphyra* was receiving something from them that was found only in the higher plants. *Salicornia ambigua*, *Tissa marina*, and *Distichlis spicata*, all of which grow in saline soils, were collected and placed in dishes in which the water was being aerated. Spores of *Porphyra* were planted upon them in order to determine whether or not they would grow on these plants as well as *Zostera*. No growth was made. *Tissa* did not live long submerged. Weak solutions of sucrose and glucose were also tried to determine if sugars in the host plants caused *Porphyra* to grow on them. This was also without success.

On July twenty-ninth, another attempt was made to grow the spores in water, to which the extracted juice of eel grass was added. Within two or three days some of the cells had divided at least once and some had started the second division (Fig. 18). A few of these had rhizoid-like outgrowths (Fig. 17). These continued alive for a week or ten days only. By this time some had formed several cells. This suggested that the former failures were probably due to the hot weather or the time of year.

On August second, the following cultures were started:

1. Sea water with unfiltered juice of *Zostera*, 2 dishes.
2. Sea water, 2 dishes.
3. Sea water with filtered juice of *Zostera*, 2 dishes.
4. Sea water with $\text{CaCl}_2 + \text{NaNO}_3 + \text{CaHPO}_4$, 1 dish.
5. Sea water aerated, 1 dish.
6. Sea water with sucrose, 1 dish.

By August 4th, 48 hours later all the spores were dead.

August 5th, more spores were planted in solutions like the above with the same results. On the whole the cultures which contained juice from *Zostera* seemed to live the longest and when growth was made did the best.

REPRODUCTION

The *Porphyras* according to Oltmann² have both asexual and sexual reproduction. The asexual reproduction is by monospores which are formed directly from the vegetative cells beginning at the tip and gradually forming toward the attached end of the frond. Hus reports them as found also among the other reproductive bodies.

The sexual reproduction is by sperms formed by a successive division of the vegetative cells to form 16, 32 or 64 sperm cells which are liberated by the breaking down of the walls; and by egg cells

² Oltmann, F., *Morphologie und Biologie der Algen*, 2. Jena, 1922.

which are hardly distinguishable from the vegetative cells. A passage way is formed from the egg to the surface of the frond. The sperin cells are carried by the waves and lodge over the egg cell. A connection is made and fusion results. The fertilized oospore divides several times forming carpospores. The development of the carpospores and monospores, Oltmann says, is the same. The carpospores were not found by the writer in *Porphyra naiadum* but are pictured by Hus. Antheridial cells were found but once by the writer (Fig. 26). The fronds are thought to be dioecious.

The fusion of the sperm and egg was observed in *Porphyra naiadum*. Cells were found, one lodged over the other; how long they had been in that position could not be determined. A passage was formed between the two (Fig. 29a). The contents of both were coarsely granular. Suddenly the contents of the upper one (sperm) started pouring into the other (egg) and in less than a minute the fusion was complete. The passage way then narrowed and closed leaving the remains of the top cell, a hull with a few granules, lying on the top of the frond (Fig. 29b). The fertilized cell rounded up noticeably. Further developments could not be determined as the cells could be kept alive no longer under the microscope. Three or four cells were seen to fuse in this manner.

Amoeboid movements mentioned by Oltmann were not observed. In one instance cells were found dividing (Figs. 32 and 33). These cells elongated and changed shape somewhat previous to dividing. What these cells were could not be determined. After division they separated, which was not true of the germinating spores on the eel grass, and they were not enclosed in the gelatinous sheath.

The work was done at the Puget Sound Biological Station under the direction of Dr. T. C. Frye, whom I wish to thank for his assistance.

SUMMARY

Porphyra naiadum is a red alga which grows on the edges of the blades of *Zostera marina* and *Phyllospadix scouleri*, the only flowering plants that grow submerged in sea water in the region of the Puget Sound Biological Station. It has a cushion-shaped base which is peculiar to this species.

The object of this paper was to investigate the cushion-shaped base and the development of the frond from it, to determine the life history, and to determine the reason that it grows only on the two host plants.

Small plates are formed on the edges of the eel grass by successive divisions of a spore in one plane. This later becomes several cells in thickness and forms a cushion. A gelatinous sheath surrounds the plant in the early stages and seems to be the only method of attachment to the host. The frond is formed from a ridge of the cells of the outside layer of the cushion.

A different type of cushion was formed in the late summer. This was an irregular mass of cells appearing as though formed from many spores which had lodged in one place. These cushions have rhizoid-like out-growths which may serve as means of attachment.

The attempts to cultivate *Porphyra naiadum* in the laboratory were mainly unsuccessful. In one or two cases the spores divided so as to form five or six cells. The juice of *Zostera* added to sea water seemed to be the most successful culture solution, which may indicate that the *Porphyra naiadum* is parasitic upon *Zostera* and *Phyllospadix*. Attempts to grow *Porphyra naiadum* on other flowering salt water plants and also on algae were unsuccessful. Aeration of the water also failed to produce any better results.

The reproduction of *Porphyra naiadum* is asexual by monospores, and sexual by sperms and eggs the fusion of which was observed. Amoeboid movements mentioned by Oltmann were not found in the spores.

PLATE 7

Porphyra naiadum Anderson

FIG. 1. Spores, thought to be monospores. $\times 300$

FIG. 2. A spore which has settled on the eel grass and become surrounded by a gelatinous sheath. $\times 300$.

FIG. 3. After first division of the spore, viewed from top surface. $\times 300$

FIG. 4. Same as above, side view. $\times 300$

FIGS. 5, 6, 7, 8, 10, 11, 13, 14. Successive stages in the formation of the plates on the edge of eel grass. $\times 300$.

FIG. 9. Side view of eight cell stage. $\times 300$

FIG. 12. Showing U-shaped manner of division of the marginal cells. $\times 300$

FIGS. 13, 14. Showing central cells of plates enlarged while more rapidly dividing marginal cells are much smaller. $\times 300$

FIG. 15. Side view of small cushion, extending to the right beyond the edge (*s*) of a blade of *Zostera*. $\times 300$.

FIG. 16. Small cushions on the edge (*s*) of the eel grass. $\times 70$.

FIG. 17. Two celled stage from culture solution, showing rhizoidal outgrowth. $\times 300$

FIG. 18. Three celled stage from culture solution. $\times 300$

FIG. 19. Longitudinal section showing the beginning of the formation of a frond (*f*). $\times 300$

FIG. 20. Irregular cushion base found on *Zostera* in August. \times about 5

FIG. 21. Small portion near edge of Fig. 20. $\times 300$

FIG. 22. Section showing formation of frond (*f*) and growth of cushion (*c*) around base of frond. $\times 300$

FIG. 23. Cross section showing formation of frond (*f*). $\times 300$

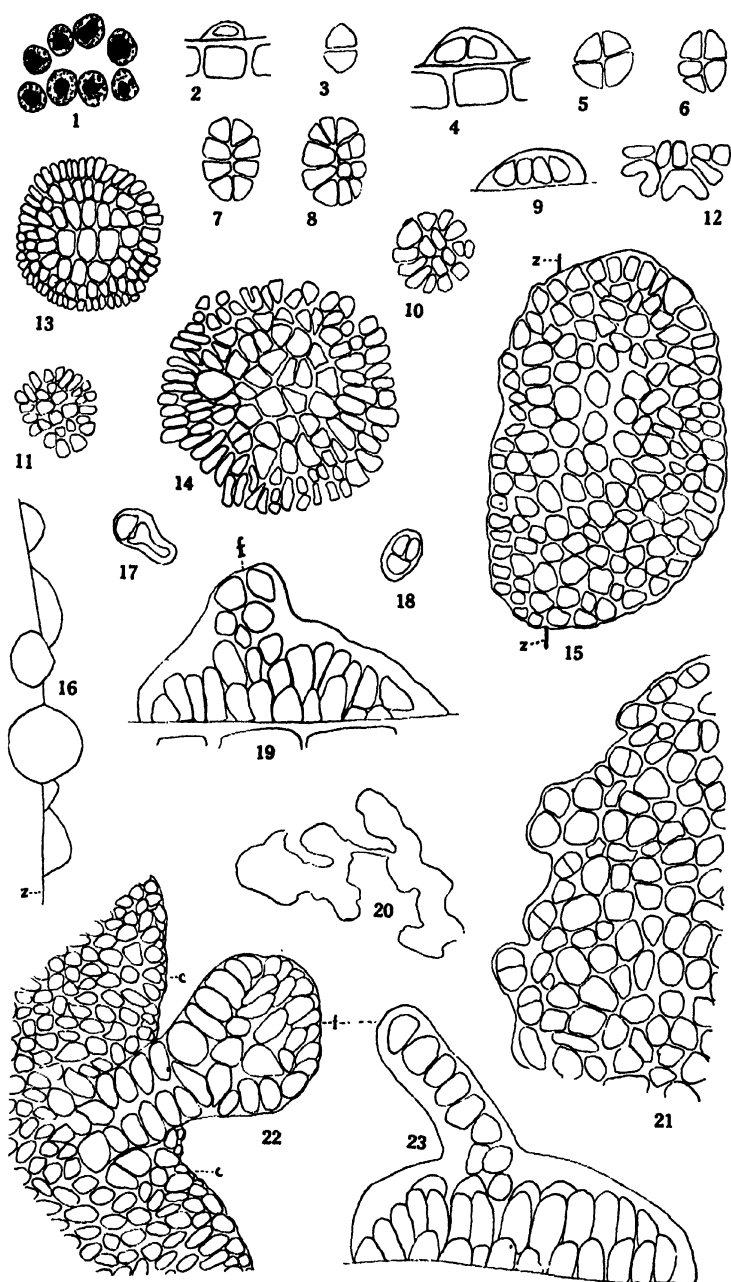


PLATE 7

PLATE 8

Porphyra naiadum Anderson

FIG. 24. Cup-like structure formed by growth of cushion (*c*) around base of frond (*f*). \times about 17

FIG. 25. Cross section of cushion and frond showing formation of frond from outer layers of cushion cells. \times 300

FIG. 26. Antheridial (*c*) and adjoining cells (*a*), with one sperm cell (*s*) which has escaped. \times 300

FIG. 27. Cross section of mature cushion. \times 300

FIG. 28. Cross section of cushion found in August showing rhizoid-like outgrowths extending through jelly at base. \times 300

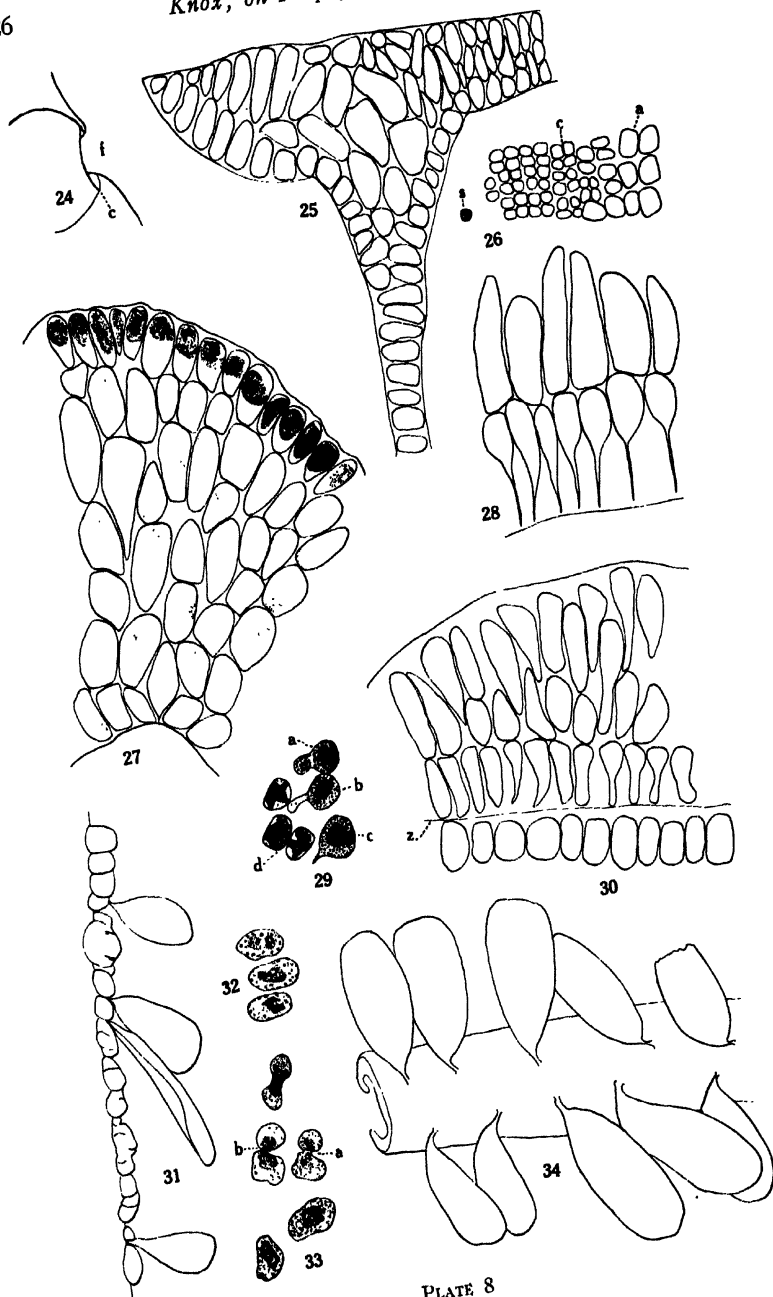
FIG. 29. Fusion of sperm and egg; (*a*) just before fusion; (*b*) after fusion; (*c*) spore beginning to round up; (*d*) adjoining cells. \times 300

FIG. 30. Section of cushion two to three layers thick; *z* is surface of Zostera. \times 300

FIG. 31. Cushion bases crowded on edge of eel grass, with a few fronds. \times about 6.

FIGS. 32 and 33. Different stages in division of cells. *b* same as *a* but twenty minutes later. \times 300

FIG. 34. Flat type of base with fronds, from the edge of eel grass. \times about 12.



A Brief Study of the Succession of Clams on a Marine Terrace

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INTRODUCTION

During the last few years much work has been done on plant and animal succession on land, but so far as can be ascertained, little has been published concerning succession in marine animal life since the classical work of Mobius. The work described in the following pages was undertaken to discover, if possible, some correlation between the change in topography and the animal succession of a given locality. The location chosen shows the formation of a marine terrace due to the eroding of a hillside by wave action (Fig. 5). This is a common phenomenon (Cleland, 1916). If a definite relationship could be shown between the two phenomena it would be of value.

In digging on a beach one not only finds living clams but also great numbers of the shells of dead individuals. The latter can be readily identified as to species. It is assumed that the animal life found upon a location serves as an indication of conditions there. "Every dominant or subdominant can be used as an indicator of past as well as present and future conditions" (Clements, 1920). It is also assumed that the shells of the dead clams serve as indicators of past conditions as living ones do of present conditions. Thus the trend of succession may be studied by comparing the distribution of the living clams with the distribution of the shells of the dead ones of the same species.

The area of greatest abundance was determined for the living individuals of each species and also for the shells of the dead clams of the same species. If these two points did not coincide, it was taken as an indication that the species was moving; that is, if it was found that the area of greatest abundance of the living clams of a certain species was farther seaward than that of the area of greatest abundance of the shells of the dead clams of the same species (represent-

ing a previous community) it was assumed that this species was moving seaward.

GENERAL DESCRIPTION OF THE LOCATION

The observations were made during the summer of 1925 on the shores of San Juan Island, near the Puget Sound Biological Station. A small triangular body of water, known locally as Argyle Lagoon, was chosen as a favorable location for the study (Fig. 1). This lagoon



Fig. 1. General view of Argyle Lagoon, San Juan Island, Washington. The picture was taken at low tide. At the point of the V-shaped spit forming two sides of the lagoon is a rocky island. The narrow channel communicating with the outside waters is shown next to the dark trees at the right. The location at which the observations were made is shown at 2.

is surrounded on two sides by a spit in the form of a V and on the third side (north) by a hill formed by a terminal moraine. The spit is formed from material eroded from the old glacial moraine forming the hill from which Fig. 1 was taken. At high tide this lagoon covers about 10 acres, at low tide about 6. It is shallow, the greatest depth is less than three meters at low tide while much of it is less than one meter.

The channel connecting the lagoon with the outside waters is narrow, about ten meters across at high tide. The deposits have filled it until the bottom is about two meters above the low tide level of the Sound waters outside. Because of this fact the lagoon is never emptied although the tidal range within is but slightly more than one meter. It is actually a huge tidal pool.

Apparently the lagoon is rapidly filling with terrigenous matter deposited in two ways: a certain amount is washed in by rain from

the hillside; the waves of the lagoon are cutting into the hillside forming a "wave cut terrace" (Cleland, 1916) at the foot of a vertical dirt bank. In addition to the terrigenous deposit, a great amount of sediment is brought in from the sea, consisting of marine deposits of decaying eel grass and algae. There is also a large amount of sawmill waste from a mill situated on the cove outside. This waste is mostly fir and pine, resinous woods. Washed into the lagoon this waste becomes waterlogged, sinks and decays. Thus the deposits from rain and wave erosion, combined with the organic deposits washed in by the sea, are rapidly converting the lagoon into dry land. At the place where the observations were made, this change seems to be taking place most rapidly.



Fig. 2. View of station 2 taken at low tide. The other two stations are nearby and are similar to this one. The waters of the lagoon are steadily cutting back into the hillside. The low bank, shown close to the fence, marks the limit of this wave action. The eroded material has formed the gently sloping beach, or marine terrace, upon which the observations were made. A strip was marked off extending from high tide level to a point as far out into the water as one could carry on digging operations. This strip one meter in width was then marked off into plots one meter square which were numbered consecutively from the mean low tide (zero) level. (see tables).



Fig. 3. View of station 2 from the shore.

METHODS

In the area chosen for the observations three stations about 15 meters apart were established (Fig. 2). Each station consisted of a strip of shore one meter in width and extending from high tide level to a point as far out into the water as digging operations could be conducted at low tide. This maximum depth was about 375 mm below mean low tide level. Each station was then divided into plots one meter square and these plots numbered successively, relative to their position up or down the slope from the low tide mark. The plot at low tide level was numbered zero (0) those above 1, 2, 3, etc. and those below, 1', 2', 3', etc. (table 1). There was difficulty in securing all the animals below low tide, so a correction was made by adding a per cent estimated as not secured. A horizontal line dividing a station so that the number of clams per square meter above, equaled the number below, was called the mean level (table 1).

The following factors were considered with reference to each station and plot: (a) The vertical distance above or below low tide of each plot. (b) The nature of the bottom material, whether it was organic deposit, sand, gravel or clay. (c) Some observations were

made as to the kind and quantity of vegetation, as algae and eel grass. (*d*) Some observations were made of the number and species of animals found on the surface of the bottom, as purple shore crabs and small striped anemones. (*e*) The surface material of each plot to a depth of 250 mm was dug up and removed with a shovel. Ordinarily 250 mm was as deep as any digging was done because in test holes dug in various places in the vicinity there was little indication of animal life below this depth. This may have been due to the action of the soil acids on the calcium carbonate of the dead shells. Each shovelful of material was sorted as dug and the clams and worms preserved. When digging in submerged areas a float was used in sorting the material and to hold the buckets and jars into which the animals were placed.

The worms were identified as to species as far as possible, and catalogued as to number and size. The living clams were sorted by species and after measuring were divided into three groups according to size, and the number in each group recorded. The same was done with the shells of the dead clams. Only the shells of the latter having both valves intact were counted, thus reducing the error due to counting shells washed in by waves or dropped by birds.

In the tables the estimated lack of efficiency of the method at each level was made and a corresponding amount is added to the figures representing the number of animals observed.

RESULTS OF EXAMINATION

On the surface there were patches of eel grass in places, particularly in station 1, but as a rule the vegetation consisted of a few tufts of *Enteromorpha prolifera* and *E. compressa*. There were also a few handfuls of *Ceremium rubrum* and occasionally some *Punctaria* on the dead eel grass. Animals were not very abundant on the mud or sandy surface, a few purple shore crabs and a species of small anemone were found.

Station 1 was the only one in which worms were numerically important. There *Nereis virens* was found throughout, from the lowest level to a height of 450 mm above low tide level. *Lanice heterobrachia* and *Lumbriconereis zonata* were also abundant as was a small red annelid, "string worm," not identified.

The following bivalves were found in all three stations: *Macoma nasuta*, *Mya arenaria*, *Macoma inquinata*, *Saxidomus giganteus* and *Cardium corbis*. Occasional individuals of the following were also

found: *Paphia staminea*, *Lyonsia californica* and *Schizothaerus nuttallii*.

With the exception of *Macoma nasuta* and *Mya arenaria* there were too few found to give data valuable for comparison so attention is given only to these two most abundant species.

In order to determine whether or not size is a factor, the following procedure was carried out (table 2). Three levels were established for each species. The levels for *Mya arenaria* were: (1) all the area more than 100 mm below low tide level; (2) the area between 100 mm below and 100 mm above low tide level; (3) all the area more than 100 mm above low tide level. The levels for *Macoma nasuta* were: (1) all the area more than 175 mm below low tide level; (2) all area between 175 mm below and 75 mm below low tide level; (3) all the area above a point 75 mm below low tide level. The living clams of each species were then divided into three groups according to size. The same procedure was carried out with the shells of the dead individuals. Comparison was then made between similar sizes of living clams and the shells of the dead clams. For example it was found that the small living *Mya arenaria* were most abundant at the highest level while the small shells of the dead *Mya arenaria* were most abundant at the medium level. On the other hand both the medium sized living *Mya arenaria* and the medium sized dead shells were found to be most abundant at the same level (—100 mm to 100 mm). This study did not show anything contrary to the previously shown tendencies; that is, the living *Mya arenaria* were found at a higher level than the shells of the dead *Mya arenaria* and the living *Macoma nasuta* were found at a lower level than the shells of the dead *Macoma nasuta*. Either the area of greatest abundance for both living and dead was found to be at the same level or the difference was in the direction expected.

The previously shown facts may be summarized as follows (table 1 and Fig. 4): (A) In reference to the *Mya arenaria* community. (a) At every station the mean level of the number of individuals per square meter of living *Mya arenaria* is found to be at a point farther shoreward than the mean level for shells of the dead of the same species. (b) At every station the area of greatest abundance of living clams is found to be farther inshore than the area of greatest abundance of the shells of the dead of this species. (c) Comparison by sizes (table 2) shows nothing contradictory to the tendencies shown in the previous data when the comparison had been made with the numbers of individuals only, without considering size.

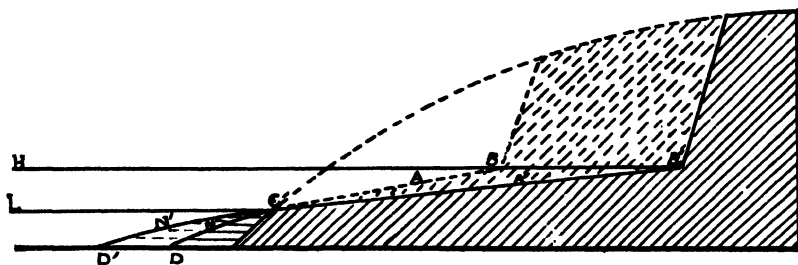


Fig. 4. Graphical illustration of the averages in table 1. The vertical distance in millimeters from low tide level is shown by the numbers below the abscissa. The distances below mean low tide level are shown to the left of the zero (0) at the bottom; the distances above are shown to the right of the zero. The shell of *Mya arenaria* is heavy and not soon disintegrated; that of *Macoma nasuta* is smaller and thinner. The former is therefore more abundant.

(B) In reference to the *Macoma nasuta* community. (a) At every station the mean level of the number of living individuals per square meter is found to be farther from shore than the mean level for the shells of the dead of the same species. (b) At every station the area of greatest abundance of living clams is found to be farther seaward than the area of greatest abundance of the dead of this species. (c) A comparison of the distribution of similar sizes (table 2) of the living with the same size of the dead of the same species gave no evidence contradictory to that shown by comparing the numbers of individuals without reference to size.

CONCLUSION

The previous data led to the conclusions that upon the area dug *Mya arenaria* is at present in greatest abundance farther landward than it was formerly, while *Macoma nasuta* is at present in greatest abundance farther seaward than it was formerly (Fig. 4 and table 1). The two species have moved, and in opposite directions. As the marine terrace grew (Fig. 4) the *Mya arenaria* optimum moved landward, while the *Macoma nasuta* optimum moved seaward.

There appears to be a definite relationship between the migration found and the probable topographical change (Fig. 5). "As waves cut back ashore, they develop a submarine terrace which extends from the base of the cliffs and slopes gently seaward until it ends abruptly in deep water. The width of such a terrace depends upon the distance that the waves have cut into the land—the *wave cut terrace*—and the distance to which the terrace has been built out by the material worn from the cliff and carried out to the edge of the rock terrace by the undertow—the *wave built terrace*." (Cleland, 1916). Upon this ter-

race there has in this case been deposited also the organic material from the water. This forms a soft organic muck deposit which varies in thickness from 250 mm at the lowest level dug, to practically nothing on the plots 500 mm above the low tide level. The compact sand of the upper levels makes an ideal environment for *Mya arenaria*, while *Macoma nasuta* is found most abundantly in organic muck (Weymouth, 1920; also observations made by the writer on other beaches of the San Juan Islands). As the beach grows flatter the clean sand is carried farther out. This sand is detrimental to *Macoma nasuta* and this species is forced farther seaward. If these conclusions are correct it is concluded that as the topography changes these two species separate, thus forming the basis for physiographic succession.

In order to confirm these conclusions the following are some of the questions that should be answered: (a) Is the deposit actually being laid down in the manner suggested? This could be ascertained by setting marked stakes at various levels and noting the amount and kind of deposit made at each from year to year. (b) Is this deposit being formed fast enough to be a factor in the migration of these species? If this factor is to be of importance this depositing action must be rather rapid as clams mature in from two to three years and probably have an average life of 10 years. (c) How long would it take for the shells of the various species to disintegrate under the influence of the soil acids, and how acid is the soil in which the clams lie? (d) Is this succession typical of all marine terraces? This could only be answered by making similar observations at other places.

The writer gratefully acknowledges the help given by many friends in the preparation of this paper. He particularly wishes to thank Dr. A. O. Weese, Dr. H. S. Brode, and Dr. V. E. Shelford for their criticism and advice.

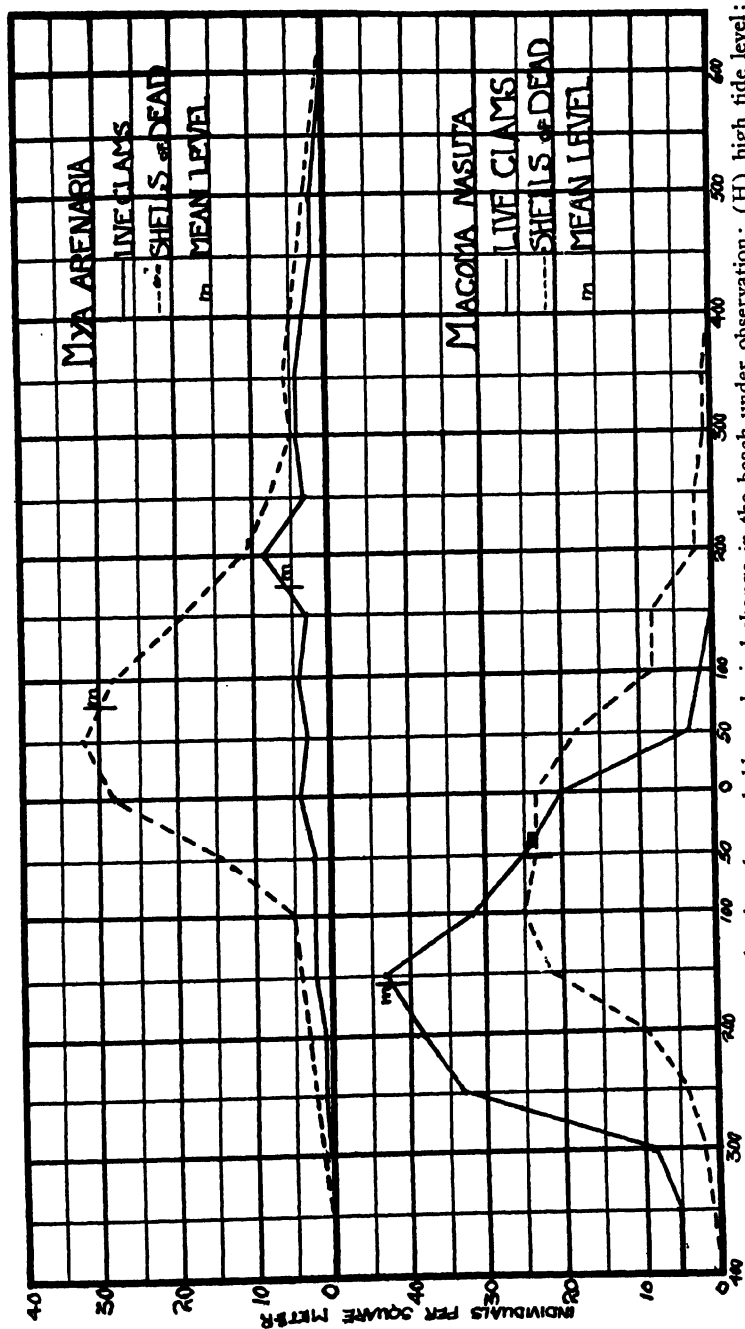


Fig. 5. Diagrammatic section showing the probable geological change in the beach under observation; (H) high tide level; (L) low tide level; (CB) original wave cut terrace; (CB') present wave cut terrace; (CD) original wave built terrace; (CD') present wave built terrace; (N) mean level of abundance of the dead shells of *Macoma nasuta*; (N') mean level of abundance of living *Macoma nasuta*; (A) mean level of abundance of dead shells of *Mya arenaria*; (A') mean level of abundance of living *Mya arenaria*. (Adapted from Cleland).

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Animal Succession on Denuded Rocks

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The present paper is the result of a series of observations made during the summer of 1925 at the Puget Sound Biological Station, Friday Harbor, Washington. Three stations were chosen representing three different types of shore; predominatingly rock, sand-gravel and mud. Rocks like those on these areas were found above the high tide line and placed at equal intervals from the high tide line downward. This was done on June 20th. Observations of the animals attached to or under the rocks were then made after 12 days, 31 days and 43 days.

At no other time were the rocks artificially disturbed in any way. Rocks 1 and 5 at station No. 2, and rock 8 at station No. 3, were dislodged by driftwood. These were replaced in their original positions as soon as discovered. Oil, dead *Ulva*, and other detritus were also removed from some of the rocks during the course of the experiments. Control observations were made on rocks adjacent to those of station No. 1, and as near as possible to those of the other stations, except that there were no control rocks available for the two lower levels of station No. 3. A more detailed description of the stations follows:

Station No. 1. East side of Brown Island. Sloping rock shore with loose rocks averaging 25 cm in diameter. About 10 meters to the north the shore became steeper and the rocks were larger. About the same distance to the south it became sandy or gravelly. Beds of *Nereocystis* were abundant off shore.

Station No. 2. East side of Brown Island, about 100 meters from Station No. 1. Sloping sand-gravel beach with very few rocks larger than 5 cm in diameter. About 15 meters to the south the shore became rocky again. The bottom off shore consisted of white sand and mud supporting a vigorous patch of *Zostera*.

Station No. 3. South end of Brown Island. Sloping muddy shore with some coarse gravel at the higher levels. A rocky reef was located about 15 meters east of this station. The shallow muddy bottom off shore was covered by a dense growth of *Ulva* and *Zostera*. This station was protected from wave action more thoroughly than

the other two on account of being on the shore side of the island instead of the channel side.

Six rocks about 25 cm in diameter were placed at each station as indicated in table 1. For summarized results see tables 2-4 and figures 1 and 2. As shown by the preliminary examination the dominant animals at the levels studied on rocky shore were *Balanus* sps. (mostly *cariosus*); *Acmaea scutum patina* Esch., *A. cassis pelta* Esch., and *A. digitalis* Esch., *Littorina sitkana* Philippi and *L. scutulata* Gould. Most other forms were represented by relatively few individuals, with the exception of the serpulids, which were found at the mean low tide line at station 1. At station 1 *Balanus* was most abundant at level 4. The same was true of station 3, but at station 2 the maximum was at level 2. As barnacles were the most abundant animals at all stations except on the lower levels of station 3, the levels of maximum animal population were as given above for *Balanus*. The maximum for *Littorina* was at level 4 of station 1, level 2 of station 2 and level 6 of station 3. *Acmaea* was most abundant at level 3 of stations 1 and 3, and level 2 of station 2.

A superficial examination three days after the beginning of the experiment showed *Littorina* on some of the rocks. Within a week very small barnacles in considerable numbers were noted in several places. *Acmaea* were the next to appear, in a little over a week, at station No. 1. No *Ulva* was found until July 2, when it was observed on two rocks at lower levels.

The first thorough examination, 12 days after the deposition of the rocks, when all levels and stations were averaged, showed the establishment of a population 38% as large as that occupying similar neighboring areas. In two instances the new population exceeded the old; at level 6 of station 1 and level 1 of station 2. In both instances the large number of newly attached juvenile barnacles accounted for the increase in numbers, as these animals constituted the greater part of the new population. However at those levels of station 1 at which *Littorina* was found, an increase was noted in this species. The genus *Acmaea* in no case approached its normal abundance.

The second examination, one month after the beginning of the experiment, gave a total population slightly greater than that indicated by preliminary observations. At levels 3 and 6 of station 1, and level 2 of station 2, the increase in barnacles was very great. At station 1, as a whole, there were nearly three times as many barnacles as there had been less than three weeks before, and nearly 50 per cent more than were observed in the preliminary census. At level 7 of

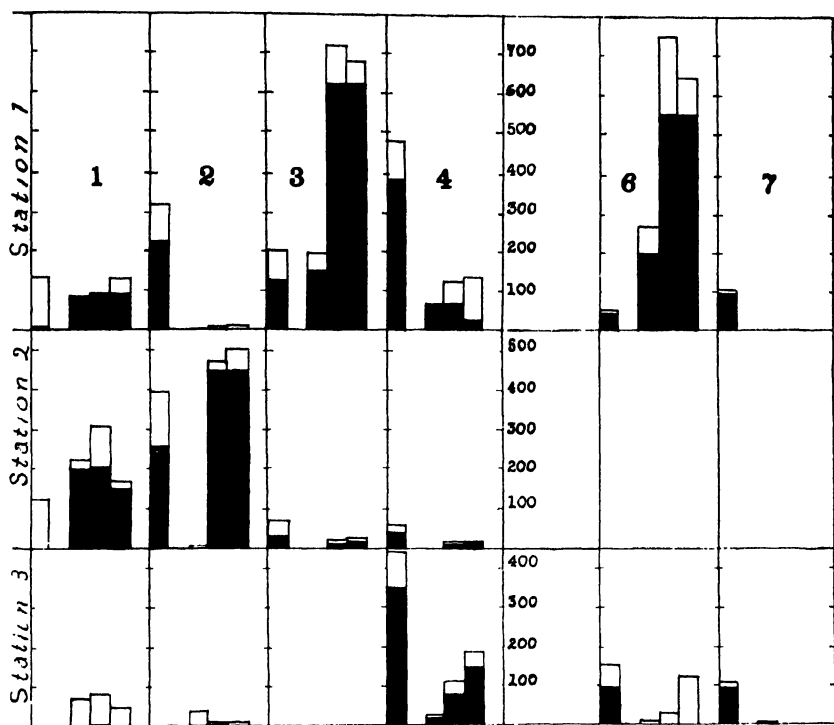


Fig. 1. Chart showing total population and *Balanus* population. In each division of the chart, the rectangle at the left indicates in black the *Balanus* population, and in white the number of all other animals present at the time of the preliminary census. The three remaining rectangles represent similarly, in order, the *Balanus* population and total population after 12, 31 and 43 days respectively. The upper row represents data as to levels 1, 2, 3, 4, 6, and 7 of station 1. The middle row shows similarly, data from station 2 at levels 1, 2, 3 and 4; in the lower row the data are given for levels 1, 2, 4, 6 and 7 of station 3.

station 1, no barnacles became established, and only a few were found above the second level at station 2. At station 3, barnacles appeared at the fourth level only, and then in relatively small numbers. *Littorina* approximately doubled in number; on the average the greatest number was reached at level 6 of station 1. *Acmaea* increased but little at station 1 and did not become established at stations 2 and 3. Station 1 showed 10 species as compared with 15 on the control rocks. At station 2 there were 6 as compared with 12 and at station 3 the ratio was 7 to 9.

The final observation, after the lapse of 43 days, showed a slight decrease in the number of *Balanus* at some stations while *Littorina*

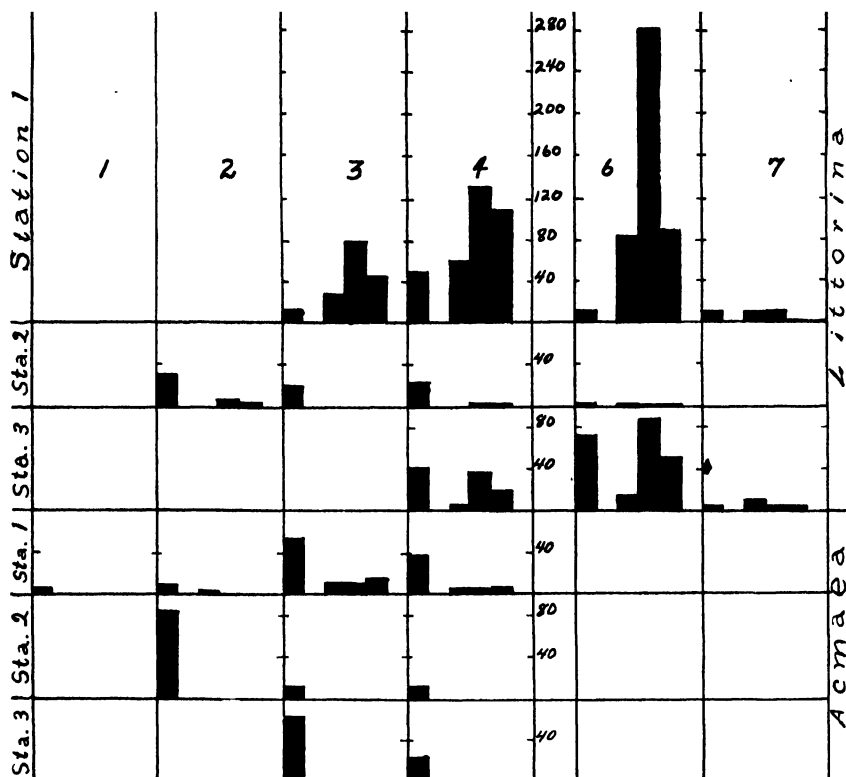


Fig. 2. Chart showing *Littorina* and *Acmaea* populations. The three upper rows represent the data as to abundance of *Littorina* and the three lower rows show similar data for *Acmaea*. See the legend of figure 1 for further explanation.

decreased in number at practically all stations. The total population decreased somewhat at most stations, bringing the average population somewhat below the normal for all stations. However no station whose total population had at any time exceeded that at the initial census, gave numbers below that value. The lower average was due to the failure of animals to gain a foothold at level 7 of station 1, levels 3, 4, and 5 of station 2, and levels 6 and 7 of station 3.

The number of species at stations 1 and 3 was the same as in the previous observation, but only six were found at station 2.

The results obtained indicate the striking rapidity with which animals of the intertidal belt colonize newly available territory. In the case of the barnacles, this colonization consists in the attachment of larval forms and their subsequent growth in place. The growth of the

barnacles may be very rapid; the largest ones observed had a basal diameter of 7.5 mm on July 21 and 9 mm on August 2. The decline in the number of barnacles at the time of the final observation indicated that some of those becoming attached at first, especially those in the more unfavorable locations, soon succumbed. The low rate of repopulation at station 3 and the upper levels of station 2 was evidently due to less favorable conditions for migration and attachment in muddy or sandy environment than in a rocky one.

TABLE 1. *Location of rocks placed on shore and conditions around them.*

Rock Number	Distance above mean low tide			Horizontal distance from No. 1			Average daily submergence during period of observation						Bottom		
	Station No.			Station No.			Station No.						Station No.		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1.....	cm 0	cm 0	cm 0	M	M	M	h 22	m 54	h 22	m 54	h 22	m 54	rock	sand	mud-shell
2.....	49	42	63	3	3	6	21	17	21	28	19	55	rock	sand	mud-sand
3.....	96	74		6	6		17	48	18	21			rock	sand	
4.....	134	119	134	9	9	12	15	52	16	02	15	52	rock	sand-gravel	mud
5.....		156			12				13					sand-gravel	
6.....	181	188	184	12	15	18	10	44	10	19	10	32	rock	gravel	mud-gravel
7.....	217		226	15		24	6				4	39	rock	rock	mud-gravel
8.....			276			30						17			sand-gravel

M, meters; m, minutes.

TABLE 2. Results of the animal census at station 1. Observations 0 are the results of the preliminary census; observations 1, 2 and 3 are the results of the succeeding counts

Level.....	1			2			3			4			6			7				
Observation....	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
Serpulidae.....	40				27				1											
Other annelids.....					8				40											
Acmaea scutum patina Esch.....	5	1			8	2	1		5											
Acmaea cassis pelta Esch.....									11											
Acmaea digitalis Esch.....																				
Mytilus edulis Linne.....																				
Mya arenaria Linne.....																				
Littorina sitkana Philippi.....									9	15	30	16	27	34	2	45	2	8	6	5
Littorina scutulata Gould.....									1	14	52	24	9	26	112	110	25	195	90	
Lacuna porrecta Carpenter.....					1				1				1							
Katherina tunicata Wood.....		1			3															
Mopalia muscosa Gould.....	1		1																	
Balanus cariosus Pallas.....	5	85	90		90	230	2	5	9	129	150	620	620	285	1	4	20	45	200	550
Amphipods.....	60				30	12	2	2	100											
Isopods.....	15																			
Pugettia gracilis Dana.....																				
Pagurus beringanus Benedict.....																				
Leptasterias hexactis Verrill.....																				
Epiactis sp.....																				
Red mites.....																				
TOTAL.....	126	87	92	121	314	6	8	11	197	188	713	674	468	66	122	136	51	270	747	644
																	105	6	5	2

TABLE 3. Results of the animal census at station 2. Observations 0 are the result of the preliminary census; observations 1, 2 and 3 are the results of the succeeding counts

Level.....	1			2			3			4			5			6								
Observation....	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3				
Serpulidae.....	4			3	1				8				11				3							
Other annelids.....					58				3								2							
Acmaea scutum patina Esch.....					23												2							
Acmaea cassis pelta Esch.....					4								1				2							
Acmaea digitalis Esch.....					11								4				2							
Mytilus edulis Linne.....																								
Mya arenaria Linne.....																								
Littorina sitkana Philippi.....					9				5				3	2		2	6							
Littorina scutulata Gould.....					22	6	1		16	1			4			1	7	1	3	6				
Lacuna porrecta Carpenter.....	2																							
Katherina tunicata Wood.....																								
Mopalia muscosa Gould.....																								
Balanus cariosus Pallas.....	200	205	150	260	450	450	450	30	2	9	15	40	10	12	30	2	4	4						
Amphipods.....	100	100	10	10	4	10	50		5	5		1												
Isopods.....	15	20			3	4																		
Pugettia gracilis Dana.....																								
Pagurus beringanus Benedict.....					1																			
Leptasterias hexactis Verrill.....				1																				
Epiactis sp.....													1				2							
Red mites.....																								
TOTAL.....	121	220	305	164	389	7	472	501	62	2	16	20	62	1	14	14	47	3	11	16	0	2	2	0

TABLE 4. Results of the animal census at station 4. Observations 0 are the results of the preliminary census; observations 1, 2 and 3 are the results of the succeeding counts

Level.....	1			2			4			6			7			8								
Observation...	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3				
Serpulidae.....	7	7	2		3	2	2																	
Other annelids.....							1		41				1											
Acmaea scutum patina Esch.....									23				4											
Acmaea cassis pelta Esch.....													1											
Acmaea digitalis Esch.....													3											
Mytilus edulis Linne.....									8				10											
Mya arenaria Linne.....							1																	
Littorina sitkana Philippi.....									18	3	28	24	21	3	17	25	2	6	1	1				
Littorina scutulata Gould.....									25	3	6	6	4	7	8	12	2			2				
Lacuna porrecta Carpenter.....	5	5	2		1																			
Katherina tunicata Wood.....																								
Mopalia muscosa Gould.....																								
Balanus cariosus Pallas.....									350	20	84	150	95	3	3	80	1	95						
Amphipods.....	60	70	40		40	10	10																	
Isopods.....																								
Pugettia gracilis Dana.....																								
Pagurus beinganus Benedict.....																								
Leptasterias hexactis Verrill.....																								
Epiactis sp.....																		1						
Red mites.....																								
TOTAL.....	*	72	82	48	*	44	14	13	465	26	118	182	156	13	29	122	105	8	1	3	0	0	0	0

*No count made.

The Gametophyte of *Soranthera Ulvoidea*

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Before 1916 little was known or understood concerning the alternation of generations in the brown algae. That year Sauvageau (Compt. Rend. Vol. 161), and the year following Kylin (Zeitschr. f. Botanik 3:43-494) published their findings on *Saccorhiza bulbosa*, *Laminaria flexicaulis*, *L. saccharina*, and *L. digitata*. Since then the development of other members of this group has been observed. Printz (K. Norske Vidensk. Selskab Skrifter 1922, pp. 1-27) followed the development of the zoospores of *Alaria pylaii* and *A. esculenta* through the gametophyte generation to sporophytes one millimeter high. From our own coast Brandt (U.S. Dept. Agric. Bull. No. 1191, Dec. 1923) reported on *Macrocystis pyrifera*, and Myers (Univ. Calif. Publ. Bot. Vol. 13, No. 3) has already published a preliminary report on *Laminaria sinclairii* and *Postelsia palmaeformis*. Only one article concerning the morphology of *Soranthera* was found (Barton, Ethel S. On the structure and development of *Soranthera*. Post. & Rupr. Jour. Proc. Linn. Soc. Bot. 33:479-486. 1897-1898).

The study of the development of the gametophyte of *Soranthera ulvoidea* was taken up in connection with a detailed study of the morphology and development of the holdfast of the same plant at the Puget Sound Biological Station during the summer of 1926. The author is indebted to Miss Margret Myers for the method of culture and to Dr. T. C. Frye for timely suggestions concerning the work.

Sea water was brought in and sterilized in quart jars in a pressure cooker. When it was cool it was aerated by pouring it back and forth from jar to jar. To each quart of water was added one small crystal each of potassium hydrogen phosphate and calcium chloride, and double the amount of sodium nitrate. The mature *Soranthera* plants were washed in clean sea water and wrapped in a clean wet cloth where they were left over night to simulate the recession of the tide. The following day they were removed from the cloth, rinsed in sterile water and placed in the covered dishes of prepared sea water.

After 24 hours the plants were removed, since it was considered that enough of the spores were shed. The culture dishes were kept in a tray of running water to guard against too great a change in temperature. The sea water at the Station is between the temperatures of 11° and 13° C. However the temperature of the cultures was about 15° and at times up to 17° C.

Twenty-four hours after the *Soranthera* plants had been removed from the culture dishes slides were examined and found to be pretty well covered with spores, many of which were germinating. Their germination is by the usual method of sending out a simple germ tube (Fig. 1).

In 84 hours many of the little plants consisted of a filament of several cells. Each cell contained a single brownish peripheral chloroplast. They continued to grow and to branch until in 9 days the plants consisted of 9 to 15 or more cells (Figs. 3-4). The diameter of the mature filament was between .008 and .009 mm.

In three weeks some plurilocular gametangia were discovered. This discovery was followed by a study of their development. They came from what appeared to be an ordinary branch starting from the side of a filament. Some of these formed two transverse walls and then developed the gametangium, thus making the gametangium rest upon a side branch of two cells. Others cut off only one cross wall which gave only one cell between the gametangium and the filament. Often this one cell was so short as to make the gametangium appear sessile. The tapering gametangium became densely packed with protoplasm. This was followed by a division of the contents crosswise and later walls were cut through at right angles to these (Fig. 8). In about 24 hours a gametangium had completed its development. On the maturity of the spores the intercepting walls disintegrated leaving the spores free within. Twenty-fours later on examining the gametangium it was found empty.

It was desirable to see and study the gametes. Hence at a time when most of the plants were bearing several gametangia a slide was removed from the culture dish and examined until a mature gametangium was found. This was brought into focus beneath the objective and the slide allowed to dry. When it was noticed that the drying began to affect the filament cold sea water was added with a medicine dropper. The gametes immediately began to emerge from the tip of the gametangium. They were of three sizes, large dark colored cells, some about half their size and not so dark and some small transparent cells. These small cells were much more active than the large dark

cells and began movement first. However in a few seconds all of the extruded gametes became quite active, the small transparent male gametes bouncing about among the larger more phlegmatic female gametes. Often when a male gamete had attached itself to a female gamete the two would revolve rapidly for a moment then dash away united. It was also observed that the medium sized gametes attached themselves to the female gametes. In some cases, not so often however, both male and female gametes would swim away alone. Fig. 12 shows the relative sizes and the difference in appearance of the gametes.

In many instances a branch came out where the empty gametangium stood and eventually pushed it off, otherwise the empty gametangia remained on the plant (Fig. 11).

Oltmann's "Algen" vol. 2 places *Soranthera ulvoidea* with the Ectocarpales because of the unilocular zoosporangia. Setchel & Gardner (Univ. Calif. Publ. Bot. 7:403) give the characteristics of a typical plant of the order Ectocarpales as the unilocular zoosporangium and plurilocular gametangia borne rarely on the same individual. The Gametophyte of *Soranthera* has the typical Ectocarpus gametangia and plant body. In fact it checks quite closely with *Ectocarpus chantransioides* described on page 406 of the above citation. The chromatophores and size of the cells in the filament agree. However, the general character of the branching does not quite agree in all respects. In the *Soranthera* gametophyte the dichotomous branching at the tips is not the rule but is found now and then. The tips of the filaments agree in that in both they are rounded and are the growing region of the plant. The gametangia are generally a little stouter than those of *E. chantransioides*, ranging from .020 to .028 mm in diameter and from .060 to .114 mm in length. The plants grown in the culture dishes did not develop the dense little tufts that characterize *E. chantransioides* but this may be due to the abnormal conditions found in the laboratory. No doubt the gametophytes would grow much more luxuriantly in their natural habitat.

At the conclusion of the nine weeks' session at the station the gametophytes were still growing and fruiting abundantly, some of the filaments having as many as eight or nine gametangia born alternately along the lower part of the branches.

PLATE 9

Magnification, $\times 350$

Fig. 1. Germinating spores 24 hours old.

Fig. 2. Germinating spores three and one-half days old. The old spore has been separated from the young gametophyte by a wall.

Figs. 3-4-5. Ten day old plants showing character of branching and increase in size.

Figs. 6-7. Thirteen day old plants showing increase in size.

Figs. 8-9. Parts of gametophytes showing the development of the gametangia. The young gametangium in 9 will soon cut off lateral cross walls which will be followed by vertical walls as shown by Fig. 8.

Fig. 10. Part of a gametophyte showing two almost mature gametangia.

Fig. 11. Part of a gametophyte, showing an empty gametangium which is being replaced by a lateral branch.

Fig. 12. Gametes, showing difference in size.

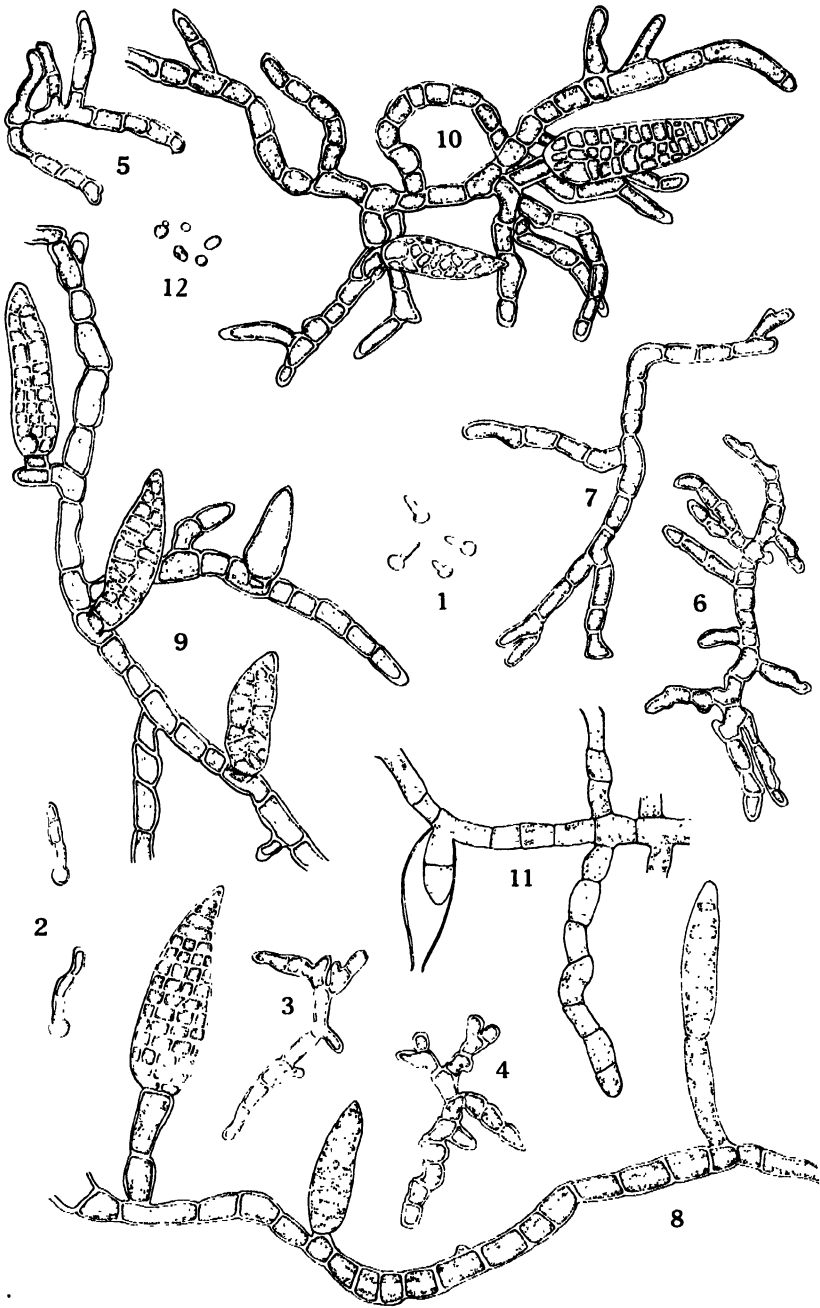


PLATE 9

The Food and Digestive Processes of *Strongylocentrotus Drobachiensis**

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Food

Strongylocentrotus drobachiensis O. F. Muller is a dominant of the Subtidal Formation in the Puget Sound region. It occurs from mean low tide level to the deepest bottom dredged in the neighborhood of the Puget Sound Biological Station (about 250 meters). Its dominance is most striking on rocky and shelly bottom, but it is found also on sandy bottom.

In an investigation of the character of the dominance of an animal, a study of its food is of very great importance. A search of the literature reveals a wide variance in reported observations as to the food of *S. drobachiensis*. The most thorough study has been made in Danish waters, where this species is also one of the dominants. It is there of lesser importance than in the Puget Sound region and does not reach the large size attained in the latter area. According to Blegvad (1915) detritus forms the principal food of this as of other dominant invertebrates of the sea bottom. He found in the alimentary tract pieces of fresh plants, dead fragments of *Zostera* and remains of animals living on plants, such as bryozoa, sponges and hydroids. Some small gastropods, Aphrodite, Gammaridae and small barnacles were also found.

Jensen (1915) examined 184 specimens from 28 localities and found them to be mainly herbivorous and carnivorous detritus eaters. He confirmed Blegvad's observations as to the prominent position of *Zostera* in their diet and found also remains of many animals among which bryozoa, sponges and hydroids were the most abundant. He added echinoderms (*Ophioglypha* sps.) and ascidians to Blegvad's list of the animals eaten. He considered the bivalve shells found by Eichelbaum to have been taken in with bottom material.

*Contribution from the Puget Sound Biological Station; and from the Zoological Laboratory of the University of Oklahoma, Second Series, No. 76.

Eichelbaum (1910) had found hydroids, polychaetes and sponges almost universally abundant, with smaller echinoids, crustacea, protozoa, diatoms, peridineae, etc., also present in considerable numbers. Pieces of lamellibranch shells were seldom absent. Remains of large plants (algae) were rarely found. He concluded that *S. drobachiensis* leads a predatory life and feeds principally upon animal food. Bottom material was present in small quantity only, evidently assisting in the mastication of the food. Eichelbaum was unable to confirm the data of various earlier workers as to the predominance of plant material in the diet, nor was he able to observe the collection of food into little pellets (Dawson, 1868). His observations were on animals from a single locality in the vicinity of Kiel. All of his individuals were small in size, 12.5-20.0 mm in diameter.

Awerinzew (1911) noted that specimens of *S. drobachiensis* in Kola Fjord varied in color from bright green-yellow to dark violet red, the latter color being found on a substratum of Lithothamnion. He ascribed the differences in color to the differences in the plant pigments ingested in the different environments, and he was able to alter the color of individuals by varying the plant food. In the Friday Harbor region *S. drobachiensis* is predominantly green in color, so much so that it is known commonly as the "green sea urchin". Specimens from the greater depths, however, may be nearly colorless, and some have a reddish or purplish tint.

Mielck (1922) calls attention to the apparent correlation between the distribution of hydroids in the Murman sea, and that of the dominant echinoderm, *S. drobachiensis*. He notes that this observation is in agreement with the previously reported findings of Eichelbaum as to the food of the sea urchin. American observations have yielded as diverse results. Dawson (1868), as noted above, recorded the formation of small round food pellets composed mostly of minute green algae, mixed with many diatoms and sponge remains. Scott (1901) made an exhaustive study of the food of the *Strongylocentrotus* of the Atlantic coast and concluded that the animal is practically omnivorous, the food at any given place depending upon what is available. In animals taken near beds of laminarian or fucoid seaweeds, the digestive tracts were almost totally filled with remains of these plants. Those obtained from sandy bottom at some distance from beds of seaweed contained, on the other hand, globular masses of sand with the remains of organisms such as are common on the bottom.

During the present study the contents of the digestive tracts of sea urchins from several different habitats in the Friday Harbor re-

gion were examined. The number of individuals was not large, but there did not seem to be much difference in the intestinal contents of animals from the same place. In all cases the food was gathered into the little pellets mentioned by Dawson and Scott. Animal remains were more abundant in specimens taken from piles, but even here there was a considerable amount of algal material. Food from specimens from wharf piles at Friday Harbor included *Balanus* shells and appendages, nauplii, copepods, wood, *Callithamnion*, and unidentified filamentous algae. From no other habitat was the food composed of as much as 50 per cent of recognizable animal matter. Urchins from the low tide line on rocky shore contained in some cases nothing but *Ulva* or nothing but *Fucus*, and in others as much as 50 per cent animal remains.

On muddy bottom specimens were obtained from 20 meters and from 50 meters. The former contained chiefly red and brown algae (including *Heterosiphonia lava*) and hydroid stems. No *Ulva* nor *Zostera* was found here. The latter depth yielded *Zostera*, *Ulva*, hydroids and unidentified plant remains. Specimens from 50 meters on shell bottom contained *Ulva*, *Zostera* (many contained practically nothing but *Zostera*), *Fucus*, unidentified red algae, diatoms and hydroid stems.

At 100 meters on shell and gravel bottom *Ulva* and *Zostera* were still the most important food organisms. Other recognized remains were *Balanus* shells and appendages, bryozoa (on laminarian algae), sponges, diatoms, *Polysiphonia* sp? and *Platythamnion* sp.? (red algae), *Pylaiella* (filamentous brown algae), and an unidentified membranous red alga. From the same depth on rocky bottom the list is practically the same. Another alga, *Desmarestia intermedia*, was identified from this series.

Two small specimens only were obtained from deeper than 100 meters. These were dredged from about 250 meters. The food seemed approximately of the same character as at 100 meters except that the particles were smaller and therefore less certainly recognizable. This may have been due in part to the small size of the urchins, but probably mostly to the fact that plant debris undergoes further decomposition in settling to the greater depths at which these animals were obtained. *Zostera* remains were however definitely recognized.

The food of *Strongylocentrotus drobachiensis* in the Puget Sound region is therefore predominantly of plant origin, consisting largely of fresh plant material in regions where such food is available in quantity, and of plant debris elsewhere. Animal food is found in great

quantity in few instances only, and then from habitats poor in plant food. The distribution of *S. drobachiensis* is not limited by that of hydroids or that of any other single food organism. The urchin is a predatory carnivore, an herbivore, or a detritus feeder as occasion demands. Food if present in sufficient quantity is not a determining factor in the distribution of this animal, and its dominance through such a large portion of the Subtidal Formation is in no small degree due to its flexibility as to food habits. The food situation for an animal feeding upon detritus is entirely different in an aquatic environment than it would be on land. In a terrestrial community an animal feeding largely or exclusively upon plants of a given species or of a given vegetation form (or their products) is limited in its distribution by the distribution of the food plants. In the sea, as far as animals feeding upon debris are concerned, this is not at all true, as the debris of plants growing near the tide-line, for example, is distributed generally over the ocean floor. Thus an animal feeding exclusively on the debris of *Zostera* might well be found from mean low tide level to a depth of some hundreds of meters, although the plant itself is limited to a very narrow vertical range.

The results of the present observations agree in the main with those of Blegvad and Petersen as to the importance of plant detritus in the food economy of *Strongylocentrotus drobachiensis*.

Blegvad (1915) in his investigation of the organic matter of the sea bottom found such detritus in the more sheltered waters to be derived almost exclusively from *Zostera*. However he found very little protein digestible with pancreatin in the detritus layer. The maximum, in the upper layer, was 68 mg. per 100 square cm. This would seem to be a very meagre source of food, but he suggested the possibility of the presence in the digestive tract of detritus eaters of enzymes reacting more powerfully upon nitrogenous matter than mammalian pancreatin. Experimental data in support of this hypothesis are however lacking.

DIGESTIVE PROCESSES

Several attempts have been made to determine the character of the digestive processes of the Echinoidea and in a few cases *Strongylocentrotus drobachiensis* has been the object of inquiry.

Cohnheim (1901) working with *Sphaerechinus granularis* was able to demonstrate a strong diastatic ferment and a weaker invertase in the intestinal mucosa (and even in the body cavity fluid under certain conditions) but could determine nothing of a positive nature in regard to the digestion or utilization of proteins.

Scott (1901) states that the digestive enzymes of *S. drobachiensis* resemble those of the pancreatic juice of mammals in that they act in neutral and alkaline media but not in acid media. Two enzymes, a slowly acting diastase and a protease could be demonstrated, and he speaks of the probable presence of a lipase. Roaf (1910) working with *Echinus esculentus* colored the food masses with various indicators and concluded that the digestive fluids in the first portion of the digestive tract were acid in reaction and that those in the latter portion gave an alkaline reaction. However, none of his reagents gave colors indicating a pH below 7.0. Gallein (9.4-14.0) and Alizarine (10.1-12.1) both gave their alkaline colors. These indicators can hardly be considered reliable under the conditions of the experiment. Neutral red (6.8-8.0) gave an intermediate tint, as did Rosolic acid (6.8-8.0); Phenolphthalein was colorless. This would indicate a pH somewhere between 7.0 and 8.0 in the initial portion of the tract.

As digestion proceeded the contents of the food pellets first became relatively acid (pH<8.0) and then more alkaline (pH>8.0). The change in pH seemed to take place at about the time the indicator diffused out of the food mass due to the progress of the digestive processes. Most of the digestion took place in the region of the junction of the inferior and superior spirals of the intestine.

pH of the digestive tract

Table 1 gives data as to the hydrogen ion concentration of digestive and other body fluids and of extracts of the digestive tract and contents, which were obtained by the use of the Stirlen and Wallace Double Wedge Comparator. The indicators used were brom thymol blue, chlor phenol red, phenol red and cresol red. No corrections have been made for salt or protein.

TABLE 1. *pH of coelom and digestive tract*

	Coelomic fluid	Extract of digestive tract
<i>S. drobachiensis</i>		
Little food.....	7.85	*7.55
Little food.....	7.6	*7.4
Some food.....	7.35	6.3
Some food.....	7.8	6.3
Much food.....	8.0	6.45
25 specimens.....	7.95	7.05
20 specimens.....	8.15	6.65
Anterior coil.....		6.3
Middle region.....		6.2
Posterior coil.....		6.6
<i>S. franciscanus</i>	7.65	6.2

*Probably contaminated with coelomic fluid.

Experiments on Digestion

Extracts of the digestive tract of the sea urchin were made by grinding the entire digestive tract, with its contents, in a mortar with sand and then adding glycerol or 95 per cent alcohol. After standing for 24 hours the liquid was filtered off by suction. In some cases, also, watery extracts were made by adding a small amount of distilled water to the ground digestive tract and filtering immediately. To the filtrate was added a small amount of toluol to retard bacterial action. This was not necessary in the case of the glycerol and alcohol extracts. No great difference was noted in the enzymes obtained by the various methods, except that the proteolytic enzyme was present in very small amounts only in the water extract.

Except in the preliminary work, the glycerol extract was used in the experiments on the digestion of egg albumen, gelatin and starch. These experiments will now be summarized:

Digestion of Albumen

To tubes containing 5 cc of the glycerol extract of the digestive tracts of 16 sea urchins was added dilute HCl and dilute Na_2CO_3 to give the pH indicated in the table below. The pH of the solutions used was determined in this and following experiments by the use of the Stirten and Wallace H-Ion Comparator with the indicators brom thymol blue, chlor phenol red, phenol red, thymol blue and cresol red for the range between pH 5.2 and pH 9.8. Below pH 5.2 use was made of the charts in Clark (1922) and brom phenol blue and methyl red in addition to thymol blue mentioned above. In each test tube were placed two Metts tubes of egg albumen. The tubes were examined and the amount of protein digested was recorded after 64 hours. The controls, at the same pH, contained boiled extract. The results in table 2 are indicated graphically in figure 1.

As will be noted, the digestion of the albumen was not a rapid process. In fact, none of the egg albumen was completely digested within the time limits of the experiment, and measurement was made of the area of discoloration and partial transparency of the egg white rather than of the amount digested out of the tube. This experiment showed the pH at which the enzyme responsible for the digestion of albumen acts most rapidly to be about 2.4, a condition never met in the digestive tract of the sea urchin. This approaches the range of optimum activity of mammalian pepsin (e. g., human pepsin, pH 1.8-2.0). A second optimum is indicated at pH 5.2. Digestion at this hydrogen ion concentration was however less rapid than in the more

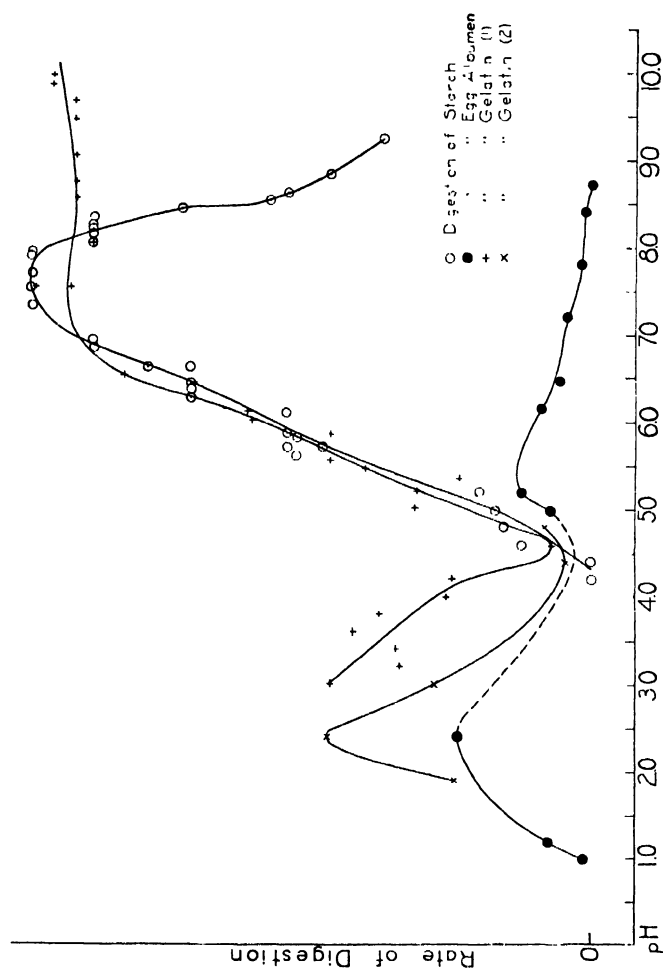


FIG. 1. The relation between hydrogen ion concentration and rate of digestion in *Strongylocentrotus drobachensis*.

acid condition. These data indicate the probable presence of two proteolytic enzymes acting upon egg albumen, the pH optima of both of which lie outside the normal pH range of the digestive tract of the animal.

Digestion of Gelatin

Experiments on the digestion of gelatin were carried out according to the method of L'ermi as modified by Palitsch and Walbum (1912) and Dernby (1918). Gelatin was made up according to the method used by Dernby, and his procedure was followed, except that the tubes were kept at approximately 37° in an improvised water bath and were cooled for examination under running water at 14° instead of in ice water. In each case to 10 cc of the gelatin solution were added 2 cc of the glycerol extract of the digestive tract and the requisite amount of dilute acid (HCl) or alkali (NaOH) to produce the desired pH. The mixture was then diluted with distilled water to 20 cc. From time to time (every 20 minutes) small amounts (1 cc) of the mixture were removed and placed in small test tubes for cooling. The condition of the gelatin was recorded after ten minutes of cooling, the scale used being that of Dernby, as follows:

- 0, Completely solid
- 1, Solid but small pieces may be torn off by strong shaking
- 2, Solid but the surface moves somewhat when the tubes are shaken
- 3, soft
- 4, half liquid
- 5, almost liquid
- 6, entirely liquid

The record of this experiment is given in table 3 and is also illustrated graphically in figure 1. The optimum pH for the digestion of gelatin is shown to be above 7.0, with no indication of a decrease in rate or completeness of proteolytic activity between this point and pH 9.8. This corresponds fairly closely to the range of activity of mammalian trypsin. It is unfortunate that the indicators available did not make possible the determination of pH values above 9.8. It is of interest to note that this experiment also indicates the presence of a second enzyme acting upon gelatin with a maximum activity at pH 2.4. This corresponds to the optimum for the enzyme noted above as acting upon egg albumen. As will be noted in the table the rate of diges-

tion here is much less than at pH 7.0 and above, and in no case was digestion carried beyond the stage indicated by the figure 2½ in the arbitrary scale, in the period of over seven hours devoted to the experiment. The curve for digestion of gelatin is very similar to that of Dernby (1 c. p. 188) illustrating the action upon gelatin of a mixture of pepsin and trypsin.

The experiments on the digestion of egg albumen and gelatin thus indicate the presence of two (or perhaps three) proteolytic enzymes. Of these the trypsin-like enzyme with an optimum of pH 8.0 and above acts rapidly and effectively upon gelatin and less rapidly upon egg albumen. (The enzyme acting upon egg albumen in an alkaline medium may not be identical with that acting upon gelatin, as different optima are indicated). The other enzyme, a weak pepsin-like ferment, with an optimum at pH 2.4, acts more rapidly upon egg albumen than does the trypsin-like enzyme. Its action upon gelatin is incomplete, however. As far as the actual digestive processes of the animal are concerned it seems, however, that the tryptic enzyme alone can be considered as functional. The presence of peptic enzymes, even in a weak form, is surprising in an animal, no part of whose digestive tract reaches a pH below 6.0. This enzyme is perhaps contained in the tissues rather than secreted into the digestive cavity corresponding thus to the autolytic pepsins found by Dernby in various animal tissues.

Digestion of Starch

Experiments on the digestion of starch were carried on in similar fashion. To 2 cc of the glycerol extract of the digestive tract were added 10 cc of water and a sufficient amount of dilute acid or alkali to produce the desired pH. The mixture was then made up to 20 cc with distilled water and 20 drops of a 2 per cent solution of starch were added. At intervals of 15 minutes a few drops of the solution were removed from each tube and dropped into a weak Iodine-Potassium Iodide solution. The degree of digestion was estimated by the color reaction and numerical values were assigned as follows: 0, dark blue; 1, reddish; 2, trace of color; 3, no color.

Table 4 is a record of the results of this experiment which are also graphically illustrated in figure 1. The optimum for the diastatic

enzyme was shown to be about pH 7.5. At this reaction the achroodextrin stage was reached in 30 minutes, while at pH 4.4 there was no diminution in the color reaction after 18 hours. At pH 9.2 the reaction was much slower than at pH 7.5, $2\frac{1}{4}$ hours being required to reach the achroodextrin stage. The optimum reaction of the amylase present in the digestive tract of *S. drobachiensis* is thus very close to the actual pH of the digestive juices, as in the case of the trypsin-like protease.

TABLE 2. *Digestion of protein*

Tube No.	pH	Amount of protein digested		Amount of protein digested in control,
		mm	mm ³	
1.....	1.2—	1.0	1.0	0.0
2.....	1.2	1.7	4.9	0.0
3.....	2.4	2.5	15.6	0.0
4.....	5.0	1.7	4.9	0.0
5.....	5.2	2.0	8.0	0.0
6.....	6.15	1.8	5.8	0.0
7.....	6.45	1.5	3.4	0.0
8.....	7.2	1.4	2.7	0.0
9.....	7.8	1.0	1.0	0.0
10.....	8.4	1.0	1.0	0.0
11.....	8.7	0.7	0.3	0.0
12.....	9.4	0.6	0.2	0.0
13.....	9.8	0.5	0.1	0.0

TABLE 4. *Digestion of starch*

Tube No.	pH	Conditions after number of minutes indicated														
		15	30	45	60	75	90	105	120	135	150	165	180	195	300	1000
1	4.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	4.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	4.6	0	0	0	0	0	0	0	0	1	1	1	1	1	3	
4	4.8	0	0	0	0	0	0	0	0	1	1	1	2	2	3	
5	5.0	0	0	0	0	0	0	0	1	1	1	1	2	2	3	
6	5.2	0	0	0	0	0	0	0	1	1	2	2	2	2	3	
7	5.6	0	0	1	1	2	2	2	3							
8	5.7	0	0	1	1	2	2	2	2	3						
9	5.7	0	1	1	1	2	2	2	3							
10	5.8	0	0	1	1	2	2	2	3							
11	5.85	0	1	1	1	2	2	2	3							
12	6.1	0	1	1	1	2	2	2	3							
13	6.25	0	1	1	2	3										
14	6.35	0	1	1	2	3										
15	6.4	0	1	1	2	3										
16	6.6	0	1	1	2	3										
17	6.6	0	1	2	3											
18	6.8	1	2	3												
19	6.9	1	2	3												
20	7.3	2	3													
21	7.5	2	3													
22	7.65	2	3													
23	7.85	2	3													
24	7.9	2	3													
25	8.0	1	2	3												
26	8.1	1	2	3												
27	8.15	1	2	3												
28	8.2	1	2	3												
29	8.3	1	2	3												
30	8.4	0	1	2	2	3										
31	8.5	0	1	2	2	2	2	2	3							
32	8.8	0	0	0	1	2	2	2	2	3						
33	8.8	0	0	0	1	2	2	2	2	3						
34	9.2	0	0	0	0	0	0	1	2	3						

SUMMARY AND CONCLUSIONS

1. *Strongylocentrotus drobachiensis* is a markedly euryoecic form, and it is a dominant over the greater part of the Subtidal Formation in the Puget Sound region, from the low tide line to a depth of 200 meters.

2. The food of *S. drobachiensis* varies widely in different parts of the world and in different habitats in the same region. In the Puget Sound region it feeds mainly upon living plants and plant debris.

3. The pH of the digestive tract varies from 6.2 to 6.6. There are present in the digestive tract two proteolytic enzymes, the optimum reaction for the one being pH 2.4 and for the other above pH 6.6. The amylase present acts most rapidly at pH 7.5. No lipase was demonstrated.

4. The presence of an enzyme for whose activity a pH outside the normal range of the hydrogen ion concentration of the organism is required is not explainable from the point of view of adaptation.

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to prevent the live box and its contents from being disturbed though frequently the egg mass was raised from the bottom of the box to the surface.

Each morning one capsule was removed and the egg mass was examined for any peculiarities that might have arisen. The individual capsules were examined in a similar way. The change in size for the whole mass was gradual and could hardly be noticed in the daily examination. In the later stages there was an occasional capsule in the egg mass in which the growth was noticeable. Then the membranes forming the capsule were greatly distended.

The capsule was removed by pinching it off where its stalk joined the central gelatinous stalk (Fig. 5): The other capsules apparently were not affected. The membranes covering the eggs seemed to be continuous with the material making up the central stalk. There was no visible sign of separation. It was thought best not to disturb the central stalk until the eggs matured. When that time arrived, the whole mass was in such a state of disintegration that the structure of the gelatinous stalk could not be determined with any accuracy.

As far as it could be ascertained, the mature embryos did not pass out of the central stalk by way of the capsular stalk. Even in the later stages, the oldest embryos were found near the center of each capsule, covered by their respective egg shells and surrounded by the gelatinous mass. If the mature embryos had passed out of the capsule by the way of the stalk, they would have been found near the stalk end, detached from the gelatinous material and the egg shells broken. None of the embryos were ever found free within the gelatinous material of the capsule. Always each egg was surrounded by its own shell. When the capsule was removed, it was put at once into a glass dish containing sea water and carried to the laboratory. The membranes of the capsule were removed, one at a time, until the gelatinous material containing the eggs was in view.

The gelatinous material containing the eggs was then put into a dish of fresh sea water. A few eggs were separated and put into a smaller dish. With dissecting needles, each shell was opened by pricking and carefully splitting it, allowing the watery albuminous fluid to flow out of the shell carrying the embryo with it.

The embryo was picked up in a pipette, put into a watch glass containing sea water and examined under the 16 millimeter objective of the compound microscope. The remaining embryos were removed in a similar way and preserved. Some of them were killed and fixed in Rouin's Solution and some in modified Carnoy's Solution. All of them were preserved in 85 per cent alcohol. Drawings of the living

embryos were made and notes on observations were taken almost every day.

From these specimens 88 slides of whole mounts were made using borax carmine for staining. Those which were not mounted were kept in 85 per cent alcohol from which sections were made later. An attempt was made to preserve and stain some of the embryos within their shells. This was not successful.

DESCRIPTION OF MATERIAL

The following descriptions of material were made from the living embryos, from the whole mounts and from sections.

Egg Mass

Each cigar-shaped "petal" or capsule was filled with eggs and attached to a central stalk of semi-transparent gelatinous material. Later each elongated capsule as well as the central stalk became covered with a yellow brown growth which had the appearance of some kind of alga. As the eggs grew each capsule became longer and wider, never spherical. In the early stages, the capsules were more slender in proportion to their circumference than in the later stages. The photographs (Figs. 1, 2 and 3) which were taken the first week in July show that the capsules were of different sizes. Each capsule was made up of five distinct parts which with a little care could be separated from each other (Fig. 6). The outer membrane, ranging in color from that of albumin to a yellow brown, was slimy, tough and thin, adhering closely to the one below. It could be shelled from the second membrane very easily with a little practice. Where this outer membrane had not darkened, the eggs could be seen lying within, and the embryos were distinct. Those embryos which were living had a more transparent color than those in which the development had been arrested. The latter showed the shells as a heavy white opaque masses (Fig. 5).

The second membrane was thicker than the first, more gelatinous and transparent. The material within could not be shelled out as in the first instance.

The third membrane was thinner than the other two, more transparent and gelatinous in nature. The second and third membranes were not as tough as the first and fourth. If care was not exercised the second and third membranes were removed at the same time.

The fourth membrane was very thin and tough, though not as tough as the first one. It was transparent and tenaciously adhered to the gelatinous mass below. It closely followed the curved outlines of the eggs within it.

The fifth part could hardly be called a membrane for it was composed of a transparent gelatinous mass of loose structure in which each egg was embedded separately (Fig. 7). It was irregular in outline, though its general shape was that of a short cigar. It was very soft in consistency although it was firm. The firmness may have been due to the eggs embedded within it.

The shell which surrounded each embryo was thin, transparent and usually almost spherical in shape. As the embryo grew the shell became more ovoid. Within the shell was a clear watery fluid in which the embryo floated. In the later stages of development the movement of the fins and mantle could be seen before the shell was removed. In the early stages the yolk could easily be distinguished from the embryo.

Not all of the embryos in each capsule were in the same stages of development. The eggs in the center of the capsule usually were more developed than those in the other parts. Although in each capsule there were eggs which had ceased developing, apparently this did not affect the growth of the other embryos. Neither did the embryos whose development had been arrested degenerate until the whole capsule disintegrated. The capsules varied in size when compared with the others at the same periods of growth, although in general the difference was not great until the last stages of development. Then there were capsules which had ceased developing several weeks before, yet were still retained on the central stalk without any apparent degeneration except the outer membrane. This outer membrane broke down in some cases in part and in others entirely, so that the second membrane was lying exposed in the water. The degeneration came from without rather than from within, because the membranes below the outer one were never affected first and the embryos were in good condition though apparently not developing. The degeneration might have been due to a yellow brown algal growth on the outer membrane. Below are the measurements of three capsules taken on June 15. They were taken from different parts of the whole egg mass. An effort was made to select those which showed the greatest differences in size. It should be said that each elongated capsule was attached to the central stalk by a stalk of its own which was a continuation of the membranes of the small egg mass. This allowed for the growth of the embryos. That is, as the capsule became larger the stalk became shorter. The eggs extended into the stalk making the capsule look more than ever like a "cigar." The measurements are as follows:

TABLE 1. *Measurements of Capsules*
Width in Centimeters

	Widest part				Stalk end				Taper end width			
	1	2	3	Av.	1	2	3	Av.	1	2	3	Av.
Capsule.....												
Egg mass.....	1.20	1.50	1.20	1.30	0.70	0.40	0.50	0.53	0.70	0.60	0.40	0.56
Distance from taper end.....	2.00	1.80	1.70	1.83								
Stalk.....	0.45	1.50	0.30	0.75								

Length in Centimeters

Capsule	Stalk	Egg mass	Taper at free end	Total length
1.....	1.50	6.00	0.60	8.10
2.....	0.50	4.50	3.50	8.50
3.....	0.50	5.00	2.10	7.60
Average.....	0.83	5.16	2.06	8.06

The average number of eggs in a capsule was 170. Two hundred seventy-eight capsules were counted. Some capsules had been removed before this study was made. In all there were at least 50,000 eggs. The variations in the developing embryo within each capsule were greater during the earlier periods than the later. The egg shell was transparent and in some cases reflected in at one end as if there were a micropyle. The space within each egg shell enlarged as the embryo grew. The shell stretched and appeared to burrow deeply into the surrounding gelatinous mass which decreased in amount causing all the eggs within the capsule to lie closer together.

The egg was oval and elastic, and floated within the shell in a transparent albuminous fluid. There was a great deal of yolk which was transparent, highly refractive, and appeared to be homogeneous. With the 4 millimeter objective of the compound microscope it was seen to be filled with fat globules of varying sizes. The protoplasm was confined to a small area of the animal pole. A layer of flat cells covered the external yolk and extended underneath the blastoderm covering the yolk. This layer of cells might be called the yolk membrane.

Embryos

The study of the embryos has been arbitrarily divided into three groups for the sake of description.

The early stages include the formation of the blastoderm and the early periods of development and growth of the organs.

The intermediate stages begin with the union of the anterior and posterior siphon folds and continue until the siphon is fully formed.

The late stages are characterized by the completion of the formation of the siphon, the appearance of chromatophores and the functioning of the various organs, i.e., discharge of ink from the ink sac, the rhythmical contraction of the hearts, the contractions of the mantle regulating the movements of the embryo.

The Early Stages of Development. In the youngest embryo observed the protoplasm was found at one end forming a germinal disc. The embryonic disc at first extended over a large part of the egg but later became more concentrated by rising from the yolk and withdrawing more to the animal pole. This gives rise to the external yolk sac (Figs. 10, 11). The embryonic disc formed an arched cap on the ovoid end of the egg. The cell walls were not well marked. The ectoderm projected a little beyond, around the entire growing edge. The arched cap area was approximately straight in outline at

its free end, arising abruptly from the sides of the egg. It was a little less than one-third of the diameter of the egg in length. The line of demarcation from this membrane and the yolk sac could easily be seen because they stained differently and the former was more transparent than the latter. With the formation of the blastoderm, two definite areas are formed in the egg; the germinal disc which forms the embryo, and the yolk sac. The yolk sac is covered by two cell layers; these are the ectoderm and the yolk epithelium. The ectoderm of the germinal disc consists of cubical cells while that in the yolk region is formed of flat cells. A middle layer, the mesoderm, is also formed about this time. It extends between the ectoderm and the yolk epithelium. The embryo can easily be distinguished from the large yolk sac.

In the embryos shown in figures 8, 9, 12 and 13, the first organ to appear from the arched thickening or cap is the rudiment of the mantle. With this elevation is a shallow depression which is the beginning of the shell gland. There is also another arched projection with a central depression lying on each side of the body below the mantle. This is the anlage of the eye. The rudiments of the tentacles appear as thick folds of the lower edge of the blastoderm.

In figures 14 and 15 the upper part of the egg is covered by the developing embryo and is constricted from the lower part which consists of the yolk covered by the yolk membrane. The external yolk is connected to the yolk sac within the embryo by a narrowing canal. The internal yolk is beginning to conform to the shape of the embryo. The whole embryo including the yolk sac increases in size during development.

The first organs to appear are the shell gland, the mantle, the eyes, the tentacles, the mouth, the siphon folds, the otocysts, the anal papilla and the ctenidia.

In figures 16 and 17 the optic stalks appear latterly as invaginated cup-like discs from which protrude the eyes with invaginated centers.

The shell gland which arises as a wide shallow pit soon forms a circular sac with a small external posterior opening. The opening eventually closes. The gland extends anteriorly and occupies a large part of the anterior dorsal side of the mantle. The very shallow disc-like mantle arises from the edges of the shell gland.

Between the mantle and the eyes are four narrow ridges. The two anterior ones are the anterior siphon folds, and the two posterior the posterior siphon folds.

The otocysts are the small circular depressions in the ectoderm which lie behind the anterior siphon folds near the optic stalks. They gradually deepen and become vesicular.

The first pairs of tentacles to become distinct are those nearest the funnel, which are the first and second pairs. The second pair reaches a higher degree of development than the first. The third pair is soon differentiated. The fourth and fifth pairs are much slower in development. The fifth pair is the last to appear and develops much less than the other tentacles. Even in the later stages they appear as two small cones lying in front of the mouth which at this time is surrounded by the five pairs of tentacles. In these figures (16, 17) the tentacles extend from the anterior surface to the head on the external yolk sac in a raised crescentic line. Three pairs of tentacles are distinguished. With the growing of the embryo from the yolk and with the gradual decrease in size of the external yolk sac a change is produced in the position of the tentacles. They slowly move from the ventral or funnel side, toward the oral or dorsal side.

The mouth arises as a transverse oval depression on the dorsal side of the embryo near the vegetative pole between the optic stalks.

The Intermediate Stages of Development. In figures 20 and 21 the external pear-shaped yolk sac is more defined. The narrow part is at the posterior end and surrounded by the developing tentacles. With the growth of the embryo a constriction forms in the region of the tentacles and a rather narrow canal arises connecting the external yolk with the internal yolk. With continued embryonic development other constrictions are made about the internal yolk. The yolk which is enclosed in the yolk epithelium does not directly communicate with the intestinal canal of the embryo. No special blood vessels are seen connecting the yolk to the rest of the body. The yolk sac lies ventrally between the mouth and the anus.

The eye stalks are conspicuous and rather wide apart. They project from the body as short thick stalks with a dark central anterior portion. The yolk within them is disappearing. The eye chamber has begun to develop. The white bodies are gradually becoming smaller.

The united anterior and posterior siphon folds are closer together and the free edges are curled toward each other. The posterior siphon folds still appear as broad rounded muscular bands (nuchal muscles). New folds have appeared laterally which extend from the posterior fold to the edge of the mantle. They are the retractor muscles of

the funnel, which aid in the formation of the lateral folds. The posterior funnel folds continue to increase in breadth. The nuchal muscles with the retractor muscles extend to the base of the mantle forming a lateral chamber which does not connect with the funnel. The funnel valve is an unpaired fold within the funnel on the side which is in contact with the body wall. The large circular otocysts are at the outer edge of the anterior folds. They increase in size rapidly and gradually change their lateral position to a more median one just dorsal to the funnel. Their walls appear to become thinner as they develop.

The mantle edges form a well marked cavity within which the anal papilla arises on the mid-line. The anal opening which lies below and in direct line with the siphonic opening is evident by the depression in the mid-line of the anal papilla. The anus is formed later by a short proctodeal invagination. The rectal valve opens directly toward the siphon. The anal papilla is the rudiment of the lower part of the alimentary tract. It gives rise to the intestine, liver and stomach.

The sac-like ctenidia lie on each side of the rectum at the bottom of the pallial cavity where they are inserted, and their free ends are pointed toward the head. They are bipectinate and are composed of lamellae which are thrown in transverse folds, and these are in turn folded to increase the respiratory surface. The pallial cavity becomes deeper as the development goes on, and the ctenidia are gradually covered by the mantle.

The fins appear as flat thickened bodies lying close to the mantle on the dorsal side. They project as two sharply defined curved flaps somewhat triangular in shape. No chromatophores are in evidence. The embryo is much larger than the one in the preceding sketch.

While the embryo is lying within the egg shell, the external yolk sac is bent acutely toward the ventral or siphon side and is about two and a half times larger than the embryo.

Figure 21 is a dorsal view. The oval mouth lies below the tentacles and a blind pouch extends from it. The tentacles are larger and bend away from the yolk.

Figures 18 and 19 illustrate a more advanced stage in development. The neck of the external yolk is more sharply defined. The ventral surface shows two pairs of the tentacles bearing suckers bent away from the yolk sac. The otocysts are becoming very large, more thin walled and are approaching the mid-line. The siphon folds have folded in nearer the mid-ventral line and the space between the united areas is becoming smaller. The ctenidia are more elongated

and the mantle covers more of the body. The ctenidia project above the mantle about half the distance farther than the rectum. The mantle is a little longer and more cup-like in shape.

On the dorsal surface (Fig. 19) the prominent eye stalks have a bilobed appearance. In the anterior part the eye is developing and the posterior part contains the white body and the optic ganglion. The amount of yolk within each eye stalk is decreasing. The mouth and the blind pouch are a little more distinct. The posterior siphon fold is curved and raised toward the anterior end in mid-line. At this stage the embryo is developing very fast and the slow, irregular contractions of the mantle are easily seen.

In figure 22 the otocysts are larger and are nearer the mid-ventral line. The anterior siphon folds have united with each other where they are in contact with the body wall. These folds have greatly elongated and extend almost to the base of the tentacles. The free edges of the siphon folds are curling around ventrally to unite along the outer mid-line. The lateral folds with the nuchal muscles and cartilage have grown larger and extend toward the base of the mantle cavity. The mantle covers about half of the ctenidia and the anal papilla. The tissues surrounding the ctenidia are beginning to take the curved irregular outline of the tissue within it. In some of the specimens the ctenidia appear to be filled with small granules.

Figure 23 illustrates the dorsal surface of figure 22.

The mouth lies between the mid-pair of tentacles and is making its way toward its adult position. The tentacles move dorsally as the embryo develops. Thus the mouth comes to lie in the position of the former external yolk sac surrounded by the tentacles.

The Later Stages of Development. Figures 24 to 27 illustrate older embryos.

The otocysts have met in mid-line. Their sides at the point of contact have a tendency to flatten. The siphon is entirely closed.

The retractor muscles extend from the posterior end of the siphon to the posterior end of the mantle. The two muscles are seen from the ventral surface, one on each side. They meet the nuchal muscles, unite with the nuchal cartilage and narrow down to rather broad flat muscular bands which hang loosely within the mantle cavity when the mantle is contracted. The lateral folds have grown and now appear as large flap-like tissues hanging from the nuchal muscles within the mantle cavity. They narrow as they approach the base of the mantle cavity and appear to be continuous at the base with the tissues covering the internal organs. The mantle is clearly

defined and functioning. It is a very muscular organ. Through its contractions and expansions it acts as a respiratory organ by drawing water into the pallial cavity and forcing it out between the funnel and the border of the mantle; it also serves as an organ of locomotion, causing the animal to move quickly through the water with a darting backward motion.

The ctenidia as well as the systemic and branchial hearts have grown. The other structures are not visible. This is due to staining and not lack of development. The four pairs of tentacles are fully formed and suckers may be found on all of them. The second pair are much longer than the others; their free edges are turned away from the yolk at a sharp angle. The whole embryo has grown longer and is now a little longer than the external yolk sac. The prominent eye stalks are decreasing and the eye itself is becoming prominent. Part of the internal structure of the mouth is seen but it is not clear enough for study.

In the living embryos many chromatophores were functioning. They varied in size as well as in color. Different cells contained different color pigments. The colors ranged from yellow-brown through brown to brown-black. More chromatophores were found at the top than at the base of the mantle. When the embryo was disturbed or excited the chromatophores were much more active and often assumed the color of the surrounding objects. Those around the edge of the mantle were a little smaller and more active than the others.

In figures 28 and 29 the embryo is approaching the period when its organs are similar to those of the adult. The external yolk sac has become smaller. The embryo is much larger and better proportioned when compared with the adult form. The head and body have grown in length and are more slender. The eye stalks have disappeared and the position of the eyes is dorso-lateral. They are in better proportion to the length of the body although they are still very large. The fifth pair of tentacles which lie over the mouth at this stage, are very small. Figure 29 is a dorsal view which shows the shape of the body stalk and the attachment of the fins. In figure 28 the ventral surface of the mantle is covered with chromatophores. The arrangement is definite. They are more evenly distributed over the ventral surface of the mantle than they have been in the earlier stages.

At this stage the mantle movements have increased in rate and are more regular in rhythm. The embryos are beginning to be very

active and move about in the dish after the egg shells have been removed.

The egg capsules are short and thick. The membranes forming the capsule are swollen and tense due to the increasing size of the embryo and the apparent absorption of moisture by the membrane.

In figures 31 and 32 the external yolk sac is greatly diminished and is gradually being absorbed into the internal yolk sac. This causes the surrounding layers to be wrinkled over the surface of the yolk. The yolk sac extends about half its length above the largest tentacle. The animal has increased in length. The large eyes are more in proportion to its head. The mouth lies more anteriorly. Figure 30 illustrates the position of the mouth in its adult position surrounded by the five pairs of tentacles after the yolk sac has been withdrawn into the body. Within the mantle many of the internal structures are seen. The ink sac filled with ink opens into the rectum. The tip of the rectum is elongated at one side into a pair of long flap-like valves. The ink is expelled at will through the funnel when the embryo is disturbed or when the sac becomes distended. It was at this stage, June 24, that the embryo was first seen to discharge the ink from the sac.

The ctenidia are longer and more branched. Lying at the base of each ctenidium is a branchial heart and an accessory heart. The systemic heart lies between the ctenidia. Pulsations were noted throughout the hearts and through the ctenidia. The ctenidia did not contract, but it seemed as if the blood flowed through the lamellae in rhythmical pulsations. The blood was colorless. The chromatophores appeared on the tentacles for the first time. They were more active over the entire surface of the animal, constantly contracting and expanding and changing in color. They were like a very beautiful electrical display. Some of the chromatophores were larger than others.

Within the mantle on each side was a very thin transparent membranous flap-like fold which we have called the lateral fold. It extended from about the center of the ctenidia to the upper surface of the mantle. The upper edge of it is made of a heavier fold and is continuous with the nuchal muscles. These structures were more or less in constant motion and appeared to have some relation to the water currents made by the action of the mantle which surrounded them. They seemed to close the mantle cavity during its contractions and thereby helped to force the water into the siphon. These folds were the shape of an elongated scoop; the broader area was near the upper end of the mantle and sloped toward the ctenidia.

Figure 30 was drawn from the hatched living embryo. In it the lateral folds are not so regular as they have been drawn. In actual life they are larger, filling the mantle cavity to a greater extent, so that they hang within the cavity in folds. Their actual form is difficult to determine accurately because of their constant activity.

Figure 33 is a median sagittal section of an embryo which is about to hatch. It is given primarily to illustrate the position of the yolk sacs. It also shows the ink sac, the rectum opening into the siphon, and the siphon valve.

In these last stages of development, the embryo has practically acquired the form of the adult. The tentacles are small. The eyes are still large. The mantle, siphon, ctenidia and rectum have almost attained their final form. The chromatophores are more like the adult appearance.

In the hatched forms the external yolk sac had almost disappeared in some of the embryos and in others, it had been entirely withdrawn into the body.

DISCUSSION

According to Korschelt and Heider (1900) the eggs of *Loligo vulgaris* are laid in gelatinous tubes attached by the ends to some firm substratum. The tubes stand out radially from their point of attachment. Each tube contained as many as 80 or more eggs. Balfour (1880) says the *Loligo* eggs are enveloped in elongated sac-like gelatinuous cords each containing about 30 or 40 eggs. The cords are attached in bunches to submarine objects. In the egg mass which has just been described the average number of eggs within each capsule was 170 which is a much larger number than those given by other authors. The number of capsules, as has been previously stated, was more than the actual count of 278. The actual number of capsules in other descriptions has not been given except that they appear in bunches.

Brooks (1880) states that the eggs of *Loligo pealii* are oval. MacBride (1914) and Korschelt and Heider (1900) say that the eggs of *Sepia* are spherical. In the present study some of the eggs were spherical; others tended to be ovoid. Those that were spherical became more ovoid with the formation of the blastoderm.

Brooks (1880) in his description of *Loglio pealii* states that the blastoderm almost covers the yolk except directly opposite the formative pole where the segmentation was initiated. Korschelt and Heider (1900) in comparing the extent of the blastoderm of *L. vulgaris* with Brooks' description of *L. pealii* state that the rudiment

of the embryo spreads over a larger area of the eggs in *L. pealii* than in *L. vulgaris*. Lankester (1906) also shows in his sketches and work that the blastoderm of the *Loligo* almost covers the entire egg. The blastoderm of these eggs in figures 12, 13, 14 and 15 cover a large area which corresponds to Brooks' description. In figure 16 the tentacles and the blastoderm cover a much smaller area of the yolk, and the tentacles are lying in the position as described by Korschelt and Heider (1900) in his description of *L. vulgaris*. They say that the tentacles arise from a circular swelling from which the tentacles later appear as button-like prominences, the first pair lying nearest the funnel. Brooks (1880) in his description of *L. pealii* states that the tentacles arise from a slight ridge or projection on each side of the embryo nearer the vegetative pole than the formative pole. In figures 14 and 15 there is a thickened area at the lower edge of the blastoderm which might correspond to the one described by Brooks (1880), but it occurs only on one side, and we have no other specimen with which to compare it. Neither have we found any stage between figures 14 and 16. It would seem as if these specimens might have characteristics of both species.

The origin of the shell gland and the mantle, and their development, is similar to the descriptions given by the authors already mentioned.

The anterior and posterior siphon folds which originate as two paired folds between the mantle and the eyes form the siphon in much the same way as it is described for the other forms.

The otocysts were found to arise as small circular depressions in the ectoderm between the anterior siphon folds and near the optic stalks. They gradually change their position as was observed in Grenacher's embryo (Lankester 1874) and come to lie in close contact with the pleuro-visceral ganglia. Kölliker (1844) and Lankester (1875) have studied the detailed structure of the otocysts.

Ray Lankester (1875) states that the eyes arise as invaginations of ectoderm which eventually close. They originate in the two lateral prominences between the mantle and the tentacles. The eyes of the embryos in question arise in the same way. The white bodies near the optic ganglia gradually diminish with the continued growth of the eye and optic ganglia.

According to Lankester (1906), the bud-like rudiments of the ctenidia appear in front of the mantle, and the folds that form the ctenidial lamellae gradually make their appearance and in turn become folded. Similar descriptions are given by Balfour (1880), Korschelt

(1892) and others. The anal papilla arises between the two ctenidia. Our specimens are in agreement with these observations.

The mouth arises as a transverse oval pit between the optic stalks near the vegetative pole and gradually changes its position as described by others until it finally comes to lie anteriorly in the space occupied by the external yolk sac and surrounded by the five pairs of tentacles.

Opinions vary regarding the origin of the chromatophores. In Grenacher's embryo (Lankester 1874) the chromatophores appear very early in the development. They are found in the blastoderm before the organs have originated. Korschelt states that they appear first on the mantle on the posterior dorsal side and are later found on the tentacles and on the head. Lankester (1906) gives a similar detailed description according to Korschelt and Heider. Girod (1884) says "that the chromatophores are derived from the mesoderm-cells which are distinguished by their large size and by their early deposit of pigment in their protoplasm. At a later stage they are covered by a thick envelope; the cells in the neighborhood stretch out into spindles and become connected with the chromatophoral cells. In this way arises the well known appearance of the contractile fibre-bundles connected radially with the chromatophoral cells. The change of shape in the pigment cells which is accompanied with a change of color was usually attributed to the contractility of these bundles, i.e., they have been regarded as muscle-fibres, while some authors have ascribed a capacity for contraction to the pigment-cells themselves, the radial fibres being considered as merely connective tissue which, it was assumed, held the actual chromatophores in position."

Joubin (1891) claims that the ectoderm-cells, which are especially distinguished by their size, sink inwards through a funnel-like depression. In the large cell at the base of the depression, the protoplasm becomes differentiated, and later, pigment appears. The cell then loses its connection with the ectoderm. A number of mesoderm-cells which could be seen even earlier regularly arranged below it, and which multiply still further, yield the radial fibres. The chromatophores would thus be due to the combined action of the outer and middle germ-layers.

In the embryos of the present study the chromatophores appeared rather late in the development as shown in figure 28. Their first appearance was on the edge of the ventral surface of the mantle. A few days later they appeared on the tentacles and still later on the head, similar to the description as given by Brooks (1890). Their detailed structure has not been studied but in figure 33 two chroma-

tophores may be seen lying below the ectoderm, where they have sunk into the mesoderm. In other sections the chromatophores are seen lying entirely in the ectoderm and are in no way connected with the mesoderm. Their origin, on this superficial examination, would appear to agree with that of Joubin.

SUMMARY

From the foregoing, it is seen that the external form of the embryo develops in the following manner:

1. The egg mass contains at least 50,000 eggs. It is composed of elongated stalked capsules attached to a central stalk. Each capsule is made up of five different parts, four membranes and a gelatinous mass of loose structure in which the eggs are embedded. The average number of eggs within a capsule is 170.

2. The blastoderm arises at the oval end of the egg as a thickened cap. This divides the embryo into two definite areas, the germinal disc and the yolk sac covered by the yolk epithelium.

3. The yolk sac which at first is a large oval body gradually becomes constricted until it divides into the external and the internal yolk which are connected by a narrow canal. The internal yolk is further sub-divided into areas formed by the constrictions of the growing embryo. The internal yolk does not communicate with the alimentary canal of the embryo. It lies ventrally between the mouth and the anus.

4. The shell gland arises as a wide shallow pit. It soon forms a circular sac with a small external opening which finally closes. The gland extends anteriorly and occupies a large part of the anterior dorsal side of the mantle.

5. The mantle arises as a shallow disc from the edges of the shell gland. It gradually increases in depth, advances toward the head and encloses the internal organs which lie within its cavity.

6. The mouth arises as an oval depression below the tentacles between the eye rudiments. It gradually moves toward the extreme anterior end, and finally occupies the position of the external yolk surrounded by the five pairs of tentacles.

7. The optic stalks appear laterally as invaginated cup-like discs from which protrude the eyes with invaginated centers. The optic stalks decrease in size while the eye becomes prominent. The eyes and optic ganglia develop at the expense of the white bodies which gradually degenerate.

8. The anterior and posterior siphon folds appear as paired narrow ridges or folds between the eyes and the mantle. One anterior siphon unites with one posterior fold, and the two united folds by their union form the siphon. The retractor muscles arise laterally and extend from the posterior folds and the nuchal muscles to the base of the mantle.

9. The otocysts arise as small circular invaginations of ectoderm between the anterior siphon folds near the optic stalk. They gradually grow larger, become thin walled and meet in the mid-ventral line below the funnel. Their sides at the point of contact have a tendency to flatten.

10. The rounded triangular fins arise on the dorsal side and are confined to the aboral fourth of the mantle.

11. The chromatophores appear late in the development of the embryo. They first appear on the ventral edge of the mantle, then on the tentacles and finally on the head.

12. The tentacles arise from the lower edge of the blastoderm as small rounded prominences. The first pair is nearest the funnel. The second pair is always larger than the other pairs, which arise in succeeding order. The fifth pair arises very late and always remains small.

13. The body of the animal is elongated and conical and the rounded triangular fins extend forward from the dorsal side and are confined to the aboral fourth of the mantle. These with other characteristics lead us to believe that these embryos belong in the family *Loliginidae* and to the genus *Loligo*.

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PLATE 10

The magnifications of the drawings are computed in millimeters from actual measurements of the embryo. In figures 8-32, two drawings of the same embryo are given illustrating opposite views. The drawings have been reduced one-half.

Figs. 1-3. Photographs of egg mass taken during the first week of July, 1925.

Fig. 4. Diagram of egg mass found attached to a rope on the fish trap.

Fig. 5. A capsule removed from the egg mass. The lower left part of capsule shows the eggs. Natural size.

Fig. 6. Longitudinal section through a capsule. Natural size.

Fig. 7. Gelatinous mass in which the eggs were embedded. Natural size.

Figs. 8-9. Opposite views of an egg within its shell. *Ma*, mantle; *Eis*, egg shell; *E*, eye rudiment; *S*, shell gland. $\times 32$.

Figs. 10-11. Early stage of blastoderm. *B*, blastoderm; *Y*, yolk. $\times 34$.

Figs. 12-13. Blastoderm almost covering the yolk. *M*, mantle; *EB*, edge of blastoderm. $\times 34$.

Figs. 14-15. Older embryo of the earlier stages. *S*, shell gland. $\times 24$.

Figs. 16-17. Embryos showing the differentiation of the shell gland, mantle, eyes, tentacles and siphon folds. *SF*, siphon fold. $\times 22$.

Fig. 18. Appearance of suckers on tentacles. *O*, otocyst; *F*, fin; *M*, mantle. $\times 32$.

Fig. 19. Dorsal view of figure 18. *Mo*, mouth. $\times 32$.

Fig. 20. Ventral view illustrating united anterior and posterior siphon folds. *A*, anal papilla; *C*, ctenidium. $\times 26$.

Fig. 21. Dorsal view of figure 20. $\times 26$.

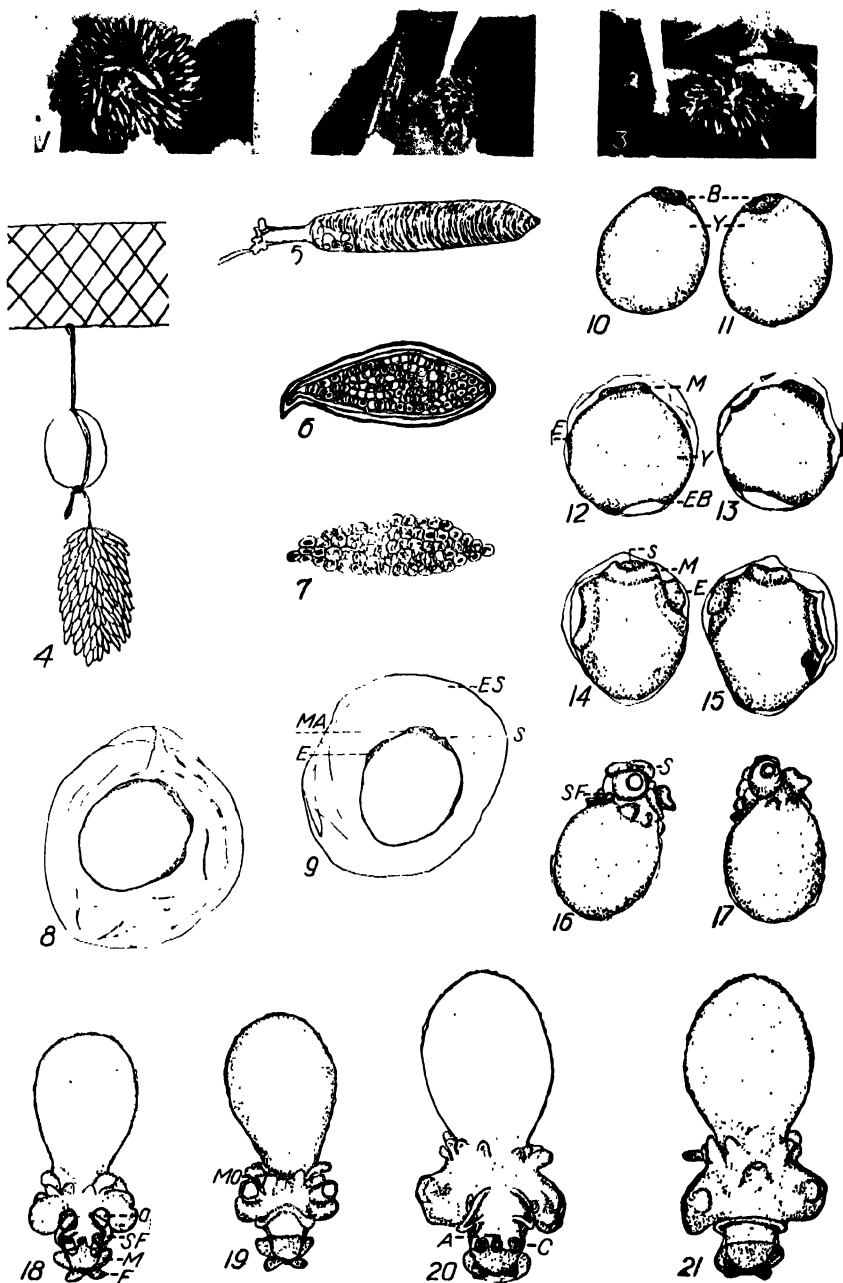


PLATE 10

PLATE 11

Fig. 22. Ventral view showing an early stage of the ctenidia. *C*, ctenidium. $\times 28$.

Fig. 23. Dorsal view of figure 22. $\times 28$.

Fig. 24. Dorsal view giving the final position of the otocysts. *BH*, branchial heart; *SH*, the systemic heart. $\times 38$.

Fig. 25. Ventral view of figure 24. $\times 38$.

Fig. 26. Ventral view of an older embryo. $\times 36$.

Fig. 27. Dorsal view of figure 26. $\times 36$.

Fig. 28. Embryo showing the arrangement of chromatophores, *CH*, over the mantle. $\times 37$.

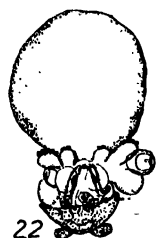
Fig. 29. Ventral view of figure 28. $\times 37$.

Fig. 30. Ventral view of hatched living embryo. *MO*, mouth; *LF*, lateral fold; *P*, pen. $\times 29$.

Fig. 31. Ventral view of embryo near time of hatching. *I*, ink sac. $\times 28$.

Fig. 32. Dorsal view of figure 31. $\times 28$.

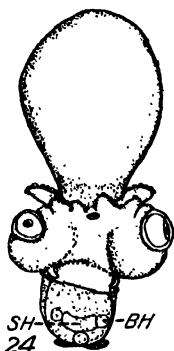
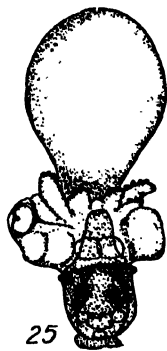
Fig. 33. Median sagittal section through an older embryo illustrating the external and internal yolk sac. *Y*, yolk. $\times 28$.



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SH-BH
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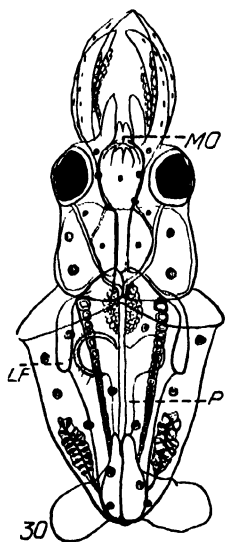
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Histology of the Retractor Muscle of *Cucumaria Miniata**

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INTRODUCTION

In preparation for physiological studies on the retractor muscle of *Cucumaria miniata* it was decided to compare it histologically with other known invertebrate and vertebrate smooth muscle. A great deal of work has been done on insect and crustacean striped muscle and on vertebrate smooth muscle but studies of lower invertebrate muscle are few.

For comparison I shall briefly outline some of the work on vertebrate muscle. McGill (1909) gave quite a comprehensive review of the German literature, and a long bibliography. The work of investigators mentioned herein whose citations are not given will be found in the bibliography of McGill (1909). Henneberg, Heidenreich, Forster, Schlater, and Soli described smooth muscle as made up of independent cells. Drasch and Schaper found it to be a syncytium. McGill (1907) found that smooth muscle arises in common with interstitial connective tissue from mesenchymal syncytium surrounding the endodermal tube in the pig embryo. Often myofibrillae and connective tissue fibres develop side by side in a single protoplasmic mass. Early writers on the structure of contracted smooth muscle held that it shortened by zig-zag folding of the fibres. Schultz considered that this condition was due to contraction in the absence of tension. Heidenhain described two types of contraction; (1) peristaltic, resulting in knots with uncontracted areas between, and (2) general or total, a shortening or contracting of the entire fibre. Later Heidenhain stated that the nucleus during contraction becomes shorter and thicker. If the resting nucleus is very slender it may wrap up into a spiral.

McGill (1909) found that vertebrate smooth muscle occurs most commonly as a syncytium, often with a rather intimate relationship between muscle and connective tissue. In early development a single muscle cell or fiber is made up of coarse fibrillae arranged peripherally about a core of protoplasm containing one or more nuclei. These fibrillae may be in a single layer or scattered through the outer part of the cell. The presence of both coarse and fine

*Contribution from the Biological Laboratory of Shorter College and from the Puget Sound Biological Station.

fibrillae in old individuals is due, she believed, to longitudinal splitting of the coarse fibrillae. Both types of fibrillae run through the anastomoses. Contraction is of the peristaltic type, that is, it involves only part of the cell, forming nodes which have a different type of staining reaction from the uncontracted fiber. (Nodes stain orange red with Mallory's aniline blue stain, while uncontracted fibrillae stain bright red). When muscle is allowed to contract in the absence of tension the fibrillae may take a wavy course.

Vertebrate smooth muscle shows a moderate amount of interfibrillar connective tissue resembling ordinary areolar connective tissue (stains blue with Mallory's aniline blue). There may also be a fine net work of collagenous fibers (also blue) and some large, wavy, homogeneous elastic fibers (stain orange tan).

Lange (1920) in discussing regeneration in the Octopus arm showed figures taken from Baliowitz. These showed the smooth muscle, long cylindrical cells tapering at each end, as made up of a peripheral layer of spirally arranged fibrillae surrounding a core of granular protoplasm containing the nucleus.

MATERIAL AND METHODS

The material used in this investigation was the red sea cucumber, *Cucumaria miniata*, attention being paid particularly to the retractor muscle and the body wall. For comparison, sections of the same structures in the white cucumber, *Cucumaria chondjelmi*, were examined as well as of the adductor muscle of *Pecten hericius*, and of the deep sea barnacle, *Balanus nublis*. Material was fixed both in a contracted and stretched condition. Some muscles were stretched and stimulated during fixation; others were stimulated to fatigue and then stretched and fixed. In all cases two muscles from the same animal, one contracted and the other stretched from three to five times its contracted length, were fixed in the following solutions: Zenker, 10% formalin, picrosulphuric acid, and Maxinow's modification of Zenker's solution.

For a study of age differences various sizes of cucumbers were used. By old cucumbers is meant individuals from 100 to 150 mm in length when the tentacles are retracted. Young ones are from 30 to 50 mm long. Some very young individuals 11 mm long were fixed whole, contracted and stretched. One tiny individual 6 mm long was preserved contracted. It was desired to trace the histogenesis of the retractor but the breeding season in 1926 was early so that all individuals collected were already spent.

The very young and tiny individuals were split in half longitudinally and both cross and longitudinal serial sections 6 microns thick were made. The retractor muscles from old and young individuals were sectioned both cross and longitudinally the same thickness. The following staining methods were applied to material from each fixing agent: iron haematoxylin with orange G; Mallory's acid fuchsin; Calleja's and Van Giesen's stains for connective tissue; Weigert's, Verhoeff's and Unna's stains for elastic fibers; Unna's muscle stain; Mallory's aniline blue and Mallory's phosphotungstic acid haematoxylin stains for differentiating between connective tissue, elastic fibers and muscle.

EXPERIMENTAL DATA

(a) *Histological appearance of muscle of all ages*

Figures 1 and 3 show cross sections of old and young retractor organs with the arrangement of elements characteristic of age differences. Figures 2 and 4 show their longitudinal arrangement. Since this organ is used as a muscle I shall first identify its parts in the terms in common usage for smooth muscle and then attempt to prove further by other methods the identity of these parts. In the cross section it can be seen that there are groups of rather large cross cut fibrillae shown in black. This group is a muscle fiber or cell (*m.c.*) made up of from 2 to 20 fibrillae (*m.f.*) arranged peripherally and enclosing the core of sarcoplasm (*s*) in which either centrally or excentrically occur one or more nuclei (fig. 1, *m.c.*).

The sarcolemma is very delicate and intimately connected with the fibers of the surrounding tissue. Between the muscle cells is a fibrous reticulum of connective tissue, (*c.f.*) with delicate fibers and many nuclei in the young, but with many dense fibers and few nuclei in the old.

The myofibrillae vary greatly in size even within a single cell. They may be large in the very young individual as well as in the old. McGill (1909) working with smooth muscle and Eycleshymer (1904), Jordan (1917) and others working with striated muscle, concluded that fine fibrillae result from the longitudinal splitting of coarse fibrillae. This may be true for the cucumber but I have found no evidence in either cross or longitudinal sections of the branching or splitting of these elements. The fibrillae of cucumber muscle are larger than those of vertebrate muscle and correspondingly fewer in number. Figures 5 and 6 from McGill (1909) show muscle fibers

(*m.c.*) from the carotid of the ox showing the arrangement of the many small fibrillae (*c.mf* and *f.mf*).

The myofibrillae appear to be homogenous with all combinations of fixing agents and stains except in one instance. In slides stained with iron haematoxylin they are black if the differentiation is not carried too far, but are grey or tan when greatly destained. In one slide out of hundreds the destaining was stopped on the border line between these two conditions and some of the fibrillae were only partly destained. These show irregular darker portions sometimes in the outer part and sometimes in the center (fig. 7 *m.f.*). I am inclined to think this is due to chemical differences in the fibril rather than to any definite structure. McGill (1909) found that contracted fibrillae hold iron haematoxylin much longer in destaining than do uncontracted fibrillae. Contraction of cucumber muscles is usually general, but may be peristaltic in some fibrillae after long stimulation with the electric current. The wavy appearance in longitudinal section is due to contraction in the absence of tension.

In old muscles the border region of a cross section differs from the central portion in several respects (compare fig. 8, *d* and *dd*, also *e* and *ee*). The myofibrillae are smaller, more numerous, and fill the cells more completely than in the central part, and the connective tissue fibers are denser and stain darker. The central part has more the appearance of a young retractor. This leads one to surmise that growth occurs in the central part and pushes the older part out so that it lies around the border throughout life.

TABLE 1. Comparative number of nuclei per unit area of .0284 sq. mm. for different ages of *Cucumaria* muscles.

Condition of muscle	Old 150 mm.	Young 50 mm.	Very young 11 mm.	Tiny 6 mm.
Contracted.....	10	34	85	97
Stretched.....	18	36	154	

In both the old and young, nuclei may be found within the muscle cells and in the connective tissue. They are fairly large and oblong and may lie with their long axes in any direction in the contracted organ, sometimes appearing round and sometimes oblong in cross sections. This similarity between muscle and connective tissue nuclei may point to a common origin of muscle cells and connective tissue from an embryonic syncytium as in vertebrates. Table 1 gives the comparative number of nuclei in a unit area of

cross section for different ages of *Cucumaria*. A unit area is the total field of the oil immersion lens with a 10X eyepiece, and is .0284 sq. mm. in area. It may be seen that the number of nuclei in a given area is inversely proportional to the age of the muscle, the tiny cucumber 6 mm in length having 97 per unit area of the retractor, and the old individual having but 10 per unit area. This relationship is shown in figure 8 also. In the stretched muscle the nuclei are correspondingly longer and more slender. When contraction occurs the nuclei get shorter and broader but no twisting occurs.

The surface of the whole muscle is covered by an epithelium-like layer composed of a fibrous reticulum with many large nuclei and a definite outer boundary. No definite cell boundaries can be demonstrated (fig. 9). There is a looser layer of connective tissue (*c.f.*) between this and the muscle cells.

(b) *Interpretation of the staining reactions.*

In studying the staining reactions of the different elements in the retractor muscle of *Cucumaria* (table 2) 10 stains were used, 5 of which gave sharp differentiation between muscle and connective tissue, the others giving negative or indifferent results. Iron haematoxylin gave good detail for studying the structure but was not differential.

(1) Mallory's acid fuchsin method calls for 1% aqueous acid fuchsin with differentiation in .25% potassium permanganate. This method should stain the contractile fibrillae of smooth muscle cells intensely red, while connective tissue cells should be brown to colorless. In *Cucumaria* the muscle fibrillae stain a greenish yellow to olive green and the connective tissue remains colorless.

(2) Calleja's method for connective tissue calls for carmine, picric acid and indigo carmine. I have been unable to find any records as to what color should be taken up by the connective tissue. This stain gives sharp differentiation between muscle and connective tissue, the former staining olive green to greenish yellow and the latter rose lavender, after Zenker. With formalin the colors are much paler.

(3) Van Gieson's method for demonstrating collagen fibrils and reticulum of connective tissue is a combination of alum haematoxylin with acid fuchsin and picric acid. This shows sharp differentiation also. Muscle stains dark olive in the old, and grey brown to rose in the young, while connective tissue stains lavender.

(4) Weigert's stain for elastic fibers calls for fuchsin, resorcin, and iron sesquichloride. Elastic fibers should appear dark blue, almost black, on a clear background. The differentiation between muscle and connective tissue is sharp but neither shows dark blue or black. Muscle stains bluish or lavender grey with the connective tissue purple.

(5) Verhoeff's elastic tissue stain, composed of haematoxylin, ferric chloride, and Lugol's solution, and counterstained with eosin, shows little contrast in cucumber muscle, both elements staining pale greyish blue to lavender. Elastic tissue should stain black while connective tissue should take the eosin stain.

(6) Unna's orcein method for elastic fibers shows little contrast. Muscle stains grey green after Zenker and pale rose grey after the other fixing reagents, with the connective tissue colorless in all cases.

(7) Unna's stain for unstriated muscle calls for polychromatic methylene blue with potassium ferricyanide for differentiation. One would suppose that the muscle would stain blue but it is pale pink after Zenker and formalin, and pale blue grey after picro-sulphuric and Maxinow, with the connective tissue a bright dark blue in all cases.

(8) Mallory's aniline blue is differential for muscle, collagen fibrils and elastic tissue. This is a combination of aniline blue, orange G, and phosphomolybdic acid. The collagen fibrils and reticulum of connective tissue should stain blue, nuclei and fibrin red, and elastic fibers pale pink or yellow. The muscle fibrillae stain brick red instead of bright red, this being due I believe to the fact that acid fuchsin stains this tissue greenish yellow instead of red. Connective tissue stains blue.

(9) Mallory's phosphotungstic acid haematoxylin combined with potassium permanganate and oxalic acid is also differential. Myoglia fibrils and fibrin should stain blue, collagen fibrils reddish brown and the coarse elastic fibrils a purplish tint. The muscle fibrillae stain blue, the connective tissue a reddish lavender and elastic fibers a bright purple.

From a study of the staining reactions I am convinced that there is a distinct difference in physico-chemical nature between echinoderm and vertebrate smooth muscle as well as a difference in physical appearance. It takes longer in many cases for the tissue to take up the stain and in some cases it never stains as deeply as vertebrate material. McGill's figure in colors of contracted cells

from the ox carotid shows the same colors as the *Cucumaria* for both muscle fibrillae (orange red) and connective tissue (blue), using the aniline blue stain. The phosphotungstic acid haematoxylin identifies the muscle fibrillae by their blue color and the elastic fibers by their deep purple. While the other stains do not show the same differential value for echinoderm tissues we may take these results as a basis for comparison with further invertebrate studies.

The muscle of the white cucumber is the same in structure and staining reactions as that of *Cucumaria miniata*. The *Pecten* muscle collected for these experiments happened to be the striated part of the adductor, and since *Balanus* muscle is strongly striated, no further work was done on either of these forms.

TABLE 2. Comparison of equal areas of muscles of different ages of *Cucumaria miniata*, from camera lucida drawings $\times 1400$.

Age of Cucumber	Condition of muscle	Length muscle	Part of muscle	Fibers per unit area	Per cent of area fibers	Average area one fiber	Reduction due to stretching
		A		B	C	D	E
Tiny	contracted	1.0 mm.	border	516	27.3	29.3 sq.mm.	
	contracted	1.0 mm.	center	445	21.4	26.7 sq.mm.	
Very young	contracted	1.4 mm.	border	496	27.0	30.4 sq.mm.	
Very young	contracted	1.4 mm.	center	348	24.0	38.0 sq.mm.	
Very young	stretched	4.1 mm.	border	2389	23.2	9.8 sq.mm.	32.0%
Very young	stretched	4.1 mm.	center	1527	27.2	9.9 sq.mm.	26.0%
Young	contracted	3.0 mm.	border	649	24.9	21.3 sq.mm.	
	contracted	3.0 mm.	center	358	18.1	28.1 sq.mm.	
	stretched	7.0 mm.	border	1177	20.0	9.4 sq.mm.	44.1%
	stretched	7.0 mm.	center	923	24.5	14.7 sq.mm.	52.3%
Old	contracted	12.0 mm.	border	409	27.8	37.7 sq.mm.	
Old	contracted	12.0 mm.	center	277	22.1	44.2 sq.mm.	
Old	stretched	62.0 mm.	border	1831	23.04	6.9 sq.mm.	18.2%
Old	stretched	62.0 mm.	center	1367	27.6	11.2 sq.mm.	25.0%

(c) Comparison of all ages contracted and stretched

The question then arises as to whether the muscle fibrillae are really the contractile elements and whether these vary with age. Change in diameter when passing from the extended to the contracted condition should be an evidence of this. Therefore both stretched and contracted muscles from the same animal were studied in cross section. It could be seen at a glance that the muscle fibrillae were distinctly smaller in the stretched muscles. The border region of a cross section also appears different from the center in both the contracted and extended muscles of the older individuals. Measurements were then made to answer the following questions and the results recorded in table 2.

- (1) What percentage of the cross sectional area is composed of muscle fibrillae? (column C).
- (2) How does the number of muscle fibrillae per unit area compare under varying conditions of age, contraction and stretching? (column B).
- (3) What is the average size of the muscle fibril in old and young, contracted and stretched? (column D).
- (4) Is there a definite ratio between the size of the muscle fibrillae after stretching and the amount the muscle was stretched? (column E).

The following procedure was used to determine this. Camera lucida drawings of the different ages of muscles both contracted and stretched were made on cards of uniform material, magnification 1400X. Figure 8 shows strips of the drawings used in this determination. The fibrillae were then cut out, counted (column B), and these and the residue weighed. Knowing the total area of the card the percentage of area occupied by the fibrillae was calculated from the percentage of weights (column C). This area divided by the number of fibrillae gives the average area of one fibril (column D). Column E gives the percentage of reduction in the average size of the muscle fibril due to the stretching.

Examining the data of table 2 we find there is more area occupied by muscle fibrillae in the border than in the center when contracted, but when stretched this condition is just reversed. In contracted muscles of all ages these fibrillae occupy on the average 27% of the border area and 21.5% of the center area. In the same muscle when stretched they occupy 22% of the border area and 26% of the center. From the histological studies the connective tissue fibers are seen to be larger and darker staining near the border. This must mean then that when the muscle is stretched the muscle fibrillae are held farther apart near the border because the connective tissue fibers really are more bulky there.

In tiny muscles the number of fibrillae per unit area in border and center are not enough different to be significant. In very young, young, and old the number in the border is progressively larger than in the center, but the fibrillae of the center region are larger in diameter than those of the border. This may mean that as the older muscle cells are pushed to the outside the larger fibrillae split up to form smaller ones, thus making the border cells have more and smaller fibrillae than the center ones. A forked or branching fibril has not been demonstrated but in the stretched muscle it can be seen

that long fibrillae pass from one cell to another showing that cucumber smooth muscle is made up of anastomosing muscle cells. The very young muscle has as large an average size of fibrillae as the old although the drawings look quite different. This is due to the fact that old muscle is made up of some large and some small fibrillae while the fibrillae of very young are more nearly uniform.

When stretched, muscle fibrillae are reduced in size proportionally to the amount of stretching, that is, when old muscle is stretched 5 times as long, the fibrillae are reduced to an average of 21% of their original size; when young muscle is stretched 2.3 times as long, its fibrillae are reduced to an average of 48% of their original size; and very young muscle stretched 3 times as long has its fibrillae reduced to 30%. This shows that these fibrillae are contractile elements.

When rested muscle is slowly stretched the fibrillae are of uniform width throughout their length but when muscle is stimulated to fatigue it contracts and will not relax of itself and also resists stretching more than the rested muscle. When slowly stretched the majority of its fibrillae are of uniform size. However some of them will not stretch but stay short and broad, and show thick, dense bands across them. Such a condition is shown in figures 10 and 11. The evenly stretched fibrillae show the ordinary orange red color with aniline blue stain, but the short thick fibrillae are dark blue shading into orange red where the ends are stretched. These short fibrillae act as though tetanically contracted from fatigue.

SUMMARY AND CONCLUSIONS

1. *Cucumaria miniata* and *Cucumaria chondjelmi* have the same type of musculature, this being different from other known types of invertebrate muscle.

2. This muscle is non-striated, its fibers being composed of from 2 to 20 large fibrillae in the periphery of a column of sarcoplasm in which may be one or more nuclei centrally or excentrically placed.

3. The muscle fibers are placed rather far apart and the space between them is filled with a reticulum of connective tissue whose fibers are few or numerous depending on the youth or old age of the individual.

4. The muscle fibrillae are identified as constituents of the muscle cell by: (a) their staining reaction as tested by different combinations of stains and fixing reagents; (b) their reduction in di-

ameter in direct proportion to the amount of extension of the muscle when relaxed.

5. The interfibrillar substance is identified as reticulum of connective tissue by its staining reactions as well as by its appearance and position.

6. The following facts show the youth to old age differences: (a) The appearance of the entire cross section of the very young muscle is uniform, in contrast to the differentiation between the border and center of the old muscle. (b) The connective tissue fibers become more numerous and stain darker as the muscle grows older. Also the border of old muscle has more and darker staining connective tissue fibers than the center. (c) The number of nuclei in the cross section of the muscle (index of living cells) varies inversely as the age of the muscle, being more numerous in the connective tissue reticulum of young muscle but fewer in the reticulum of old muscle, that is, in the old muscles the increase of reticular fibers is correlated with a decrease of nuclei or living cells. (d) The same relationship holds for fibers and nuclei of connective tissue between border and center of old muscle as between young and old individuals.

7. Since the percentage of the volume of the muscle which is muscle fibrillae is practically the same in all ages, and since the living connective tissue cells (nuclei) are numerous, with few fibers in the young but just the opposite of this in the old, we may conclude that old age is measured by an increase of intercellular connective tissue fibers at the expense of living cells; that is, there are fewer living cells per gram weight in the old to carry on metabolic processes.

8. Experiments with stains show that there is some physico-chemical difference between vertebrate and invertebrate smooth muscle.

I wish to thank Dr. E. J. Lund of the University of Texas, at whose suggestion this work was undertaken, for his many helpful discussions and criticisms. I also wish to thank Dr. T. C. Frye of the Puget Sound Biological Station for the opportunities given me to collect material for this work.

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PLATE 12

Fig. 1. Young retractor muscle, cross section; Zenker, Mallory's aniline blue; *c.t.* connective tissue fibers; *c.t.n.* connective tissue nucleus; *m.c.* muscle cell; *m.f.* muscle fibrillae; *n.* nucleus of a muscle cell; *s.* sarcoplasm. $\times 628$.

Fig. 2. Same as 1. longitudinal section.

Fig. 3. Old retractor muscle, cross section; Zenker, Mallory's aniline blue; lettering as in Fig. 1. $\times 628$.

Fig. 4. Same as 3. longitudinal section.

Fig. 5. Cross section of smooth muscle cells from the carotid of the ox, after McGill; iron haematoxylin; *c.mf.* coarse myofibrillae; *c.n.* contraction node; *c.nu.* contracted nucleus; *f.mf.* fine myofibrillae; *i.c.* interstitial connective tissue; *m.c.* muscle cell; *m.f.* myofibrillae in uncontracted internodal region; *r.nu.* resting nucleus; $\times 1480$ but reduction in printing not known.

Fig. 6. Same as 5, longitudinal section; $\times 290$, but reduction in printing not known.

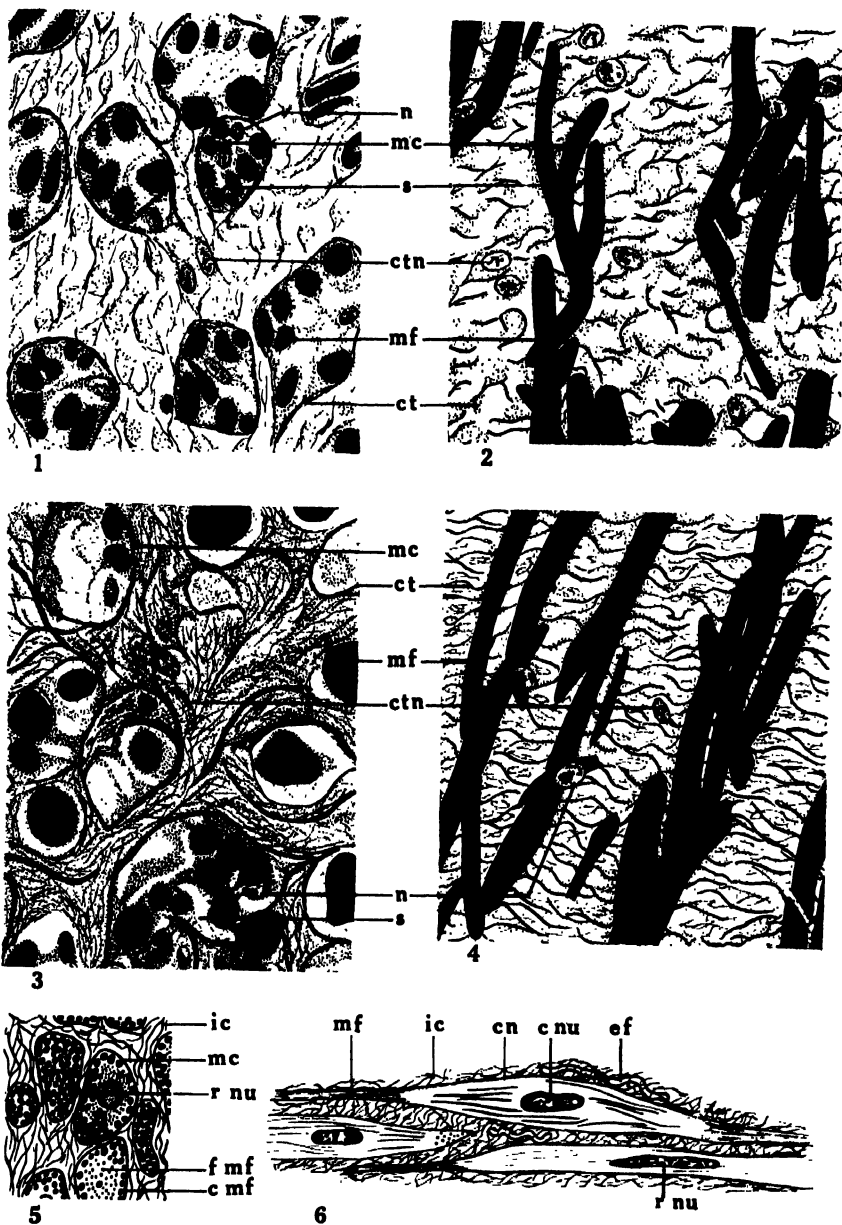


PLATE 12

PLATE 13

Fig. 7. Old retractor muscle, cross section; formalin, iron haematoxylin and orange G; *m.f.* fibrillae partially destained. $\times 653$.

Fig. 8. Comparison of muscle fibrillae and nuclei of retractor muscle in all ages of *Cucumaria*, contracted and stretched. $\times 653$.

- a* border, *aa* center region of tiny individual contracted
- b* border, *bb* center region of young individual contracted
- c* border, *cc* center region of young individual stretched
- d* border, *dd* center region of old individual contracted
- e* border, *ee* center region of old individual stretched

Fig. 9. Covering layer of young retractor muscle; formalin, Van Giesen; *co.* covering layer; *c.t.* connective tissue fibers; *m.c.* muscle cell. $\times 653$.

Fig. 10. Cross section of old muscle stimulated to fatigue and stretched to five times its contracted length; *t.m.* fibrillae showing greatly swelled regions; Zenker, Mallory's aniline blue. $\times 653$.

Fig. 11. Same as 10 longitudinal section.

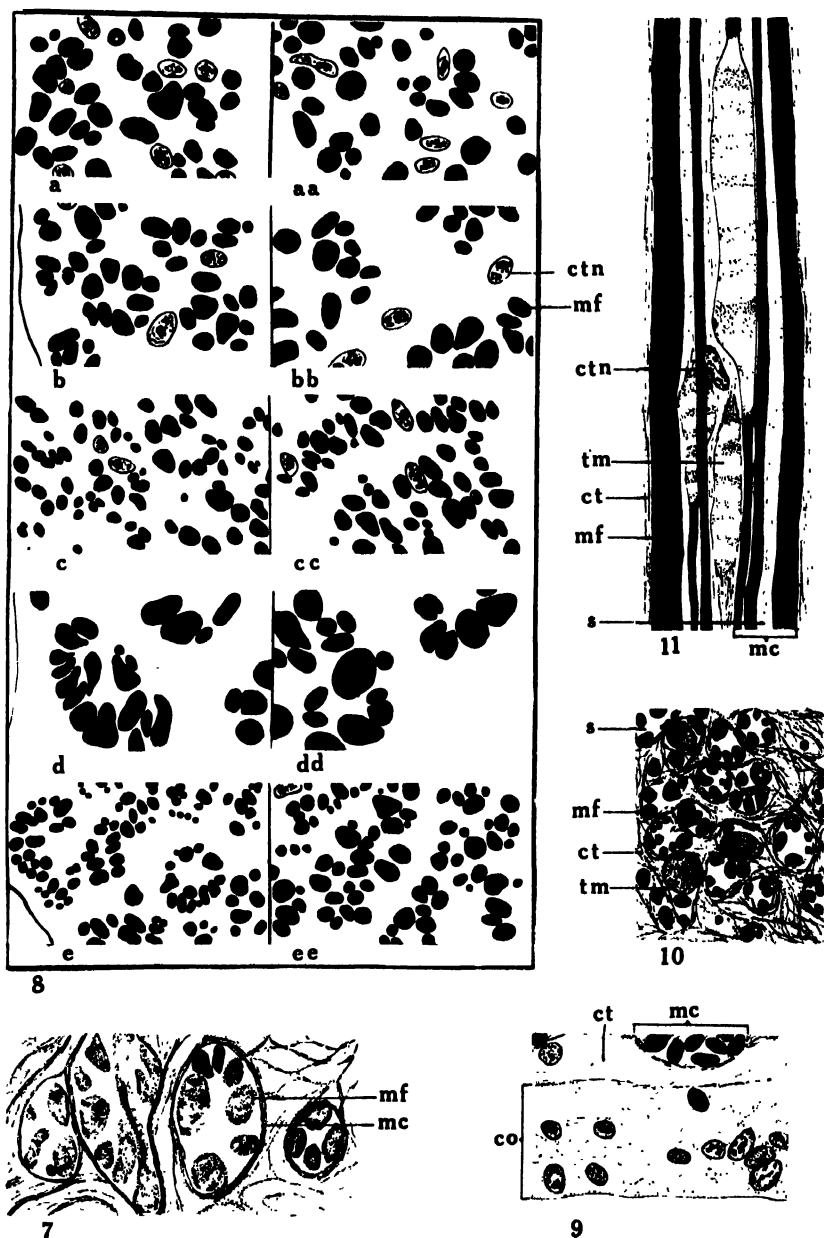


PLATE 13

A New Ectoparasitic Trematode From the Dogfish Shark (*Squalus Sucklii*)

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Onchocotyle striata, a new species of trematode described in this paper, was found in moderate numbers on the gills of the dogfish shark, *Squalus sucklii* (Girard) in the summer of 1927, during studies carried on at the Puget Sound Biological Station, Friday Harbor, Washington. To Dr. John E. Guberlet, under whose direction this study was made, I wish to express my appreciation and deepest gratitude for help and suggestions without which this paper would have been impossible.

Onchocotyle striata clearly belongs to the genus *Onchocotyle*, created first by Diesing in 1850 and continued by Van Beneden in 1853 (after synopsis of literature by Cerfontaine). It has the characteristic posterior fixation disc with three pairs of suckers armed with hooks. A fourth pair of suckers in the structure constituting the appendix has no hooks in the suckers, but possesses a tiny pair at their base. There is an anterior sucker without hooks, and the digestive crura are typically in two lobes.

The specimens were studied alive, and then were killed in Carnoy's solution or in Bouin's fluid. For both whole mounts and for sections, the trematodes were stained with Ehrlich's or Delafield's haematoxylin and destained in acid alcohol. The sections were counterstained with eosin.

GENERAL APPEARANCE

This species (Fig. 1) is small in size, varying from 4 to 5.5 mm in length, depending on the state of contraction. Measurements were made from the anterior tip of the oral sucker to the posterior tip of the appendix. *O. striata* lies among the gills of the dogfish with the fixation disc securely attached to the tissues. The anterior end protrudes into the gill chamber and is free to move in any plane. Living specimens are opaque white, with the digestive system conspicuous as two greenish-brown or reddish-brown bands running the length of the body. Under the microscope the living animal is slightly transparent, while the vitellaria are opaque. The worm attaches to

the gills by means of the characteristic sucking disc which is composed of three pairs of suckers, each armed with a hook. The appendix, which has two small suckers and a pair of tiny hooks between them, points directly posterior, while the body proper points anteriorly, the disc acting as sort of a pivot. Each sucker in the disc is capable of being extended some distance and rotated in any plane regardless of the activity of the others. When the suckers are extended in this way, they give a stalked appearance. Likewise, each hook is capable of being protruded or retracted independently of the others. The small suckers in the appendix are capable of extension also; they diverge when this occurs, taking a Y-shape. The appendix arises from the dorsal side of the body; however, as the worm attaches the dorsal surface of the fixation disc to the gill, this makes the dorsal side of the body occupy a ventral position and lie undermost, while the morphologically ventral surface occupies a dorsal position. As the body is extremely contractile, it is capable of an extension of four to five times its usual length. The cuticle is striated transversely by small grooves or folds which are regular and numerous in normal animals, but which in extreme extension disappear entirely. It is from the striated appearance caused by these tiny convolutions in the cuticle that *O. striata* received its name. These are not figured by Causey (1926) in *O. somniosi*, nor mentioned in any other form previously described. The body tapers gradually toward the anterior end, swells out in the middle, and is abruptly constricted at the posterior end where it joins the fixation disc. In cross section, the body is seen to be rather convex on the dorsal side and flat on the ventral.

ORGANS OF ATTACHMENT

An anterior sucker is present (Fig. 1) around the mouth cavity. It has a thin lip and is subterminal.

The fixation disc is oval (Fig. 1) bearing three pairs of suckers which are rounded and each about the same size as the anterior sucker. A thin lip also surrounds each of these suckers. There is a crescent-shaped hook (Fig. 2), 1045 micra in length, which lies imbedded in the sucker, only the sharp bent prong on one end protruding. The hooks are so located and the prong on the end so turned that each points toward the anterior end of the body and toward the mouth of the sucker. The hooks are solid, highly refractive and have on each side a small median groove which runs the whole length. A double row of tiny spines, not uniform in size, is located on each side of the hook near the end bearing the prong. There are about 12 of these spines in one row, and 5 or 6 in the other.

The appendix (Fig. 1) which arises dorsally from the fixation disc, bears a pair of very small suckers without hooks. Since the mouth is narrow and has no lip, "each sucker has the shape of a water-melon," according to Goto (1894:27), "with a constriction at the posterior part." There are two very minute hooks (Fig. 3) imbedded between the bases of the suckers. These hooks are triradiate; one of the prongs is very long and sharp, while the other two are dull and rounded. The appendix is cylindrical and has definite striations in the cuticle, like those on the rest of the body. This organ is transparent, except for the branch of the intestine which projects into it for nearly the whole length, and is obvious from its dark contents.

DIGESTIVE SYSTEM

The form of the digestive system (Fig. 4) may easily be seen in living specimens or in cleared but unstained whole mounts. A mouth, pharynx, esophagus and branched intestine constitute the digestive system. The mouth is situated on the ventral side of the anterior end of the body, in the base of the anterior sucker. It opens into the ellipsoidal, muscular pharynx through a small tube, which continues small while traversing the pharynx. This small tubular canal opens into the esophagus which is fairly long and large, and has a ventral diverticulum which projects anteriorly under the pharynx as a sort of blind pouch. The esophagus leads to the two intestinal crura which arise immediately from it and proceed posteriorly nearly to the level of the fixation disc where they reunite. Shortly posterior to the union of the trunks, the digestive canal gives off two small branches, one of which continues posteriorly into the fixation disc to the level of the third pair of suckers. The second branch enters the appendix and ends shortly before reaching the level of the suckers. Both terminations appear to be blind pouches. The crura are simple tubes for a short distance after branching from the esophagus but soon become convoluted, giving off irregular lobes or diverticula which extend out to the sides of the body, and are larger and more numerous on the outside than on the inside. They become a simple tube at the posterior union of the crura.

EXCRETORY SYSTEM

The excretory system (Fig. 5) is difficult to demonstrate in any but a living specimen. If a worm is placed under a cover slip and viewed with a microscope, the anterior and posterior ends of the excretory canals may easily be traced by the beating of the cilia which

line the walls of the entire system. There are two vessels on each side of the body, running along near the dorsal surface. Of the two vessels, the larger one on each side opens to the exterior on the dorsal side, anterior to the genital pore, near the lateral border. The posterior portion of the excretory system may be seen to extend well into the sucking disc, where the larger vessel unites with the smaller one after many convolutions. The smaller vessel on each side of the body may be considered the beginning of the excretory canal where it arises near the anterior sucker. It pursues a winding course down each side of the body to the disc, turns, and enlarges, becoming the larger vessel, continuing its course to the anterior region of the body where it opens to the exterior in the manner already described. A small branch may be seen extending into each side of the appendix to the level of the suckers, where each branch turns and winds back upon itself to the main canal. Small branches are also given off to each sucker in the disc.

REPRODUCTIVE SYSTEM

The genital pore is situated ventrally, somewhat posterior to the pharynx and in the median line of the body. Situated on each side of the genital pore are the two openings of the gavinac.

The male reproductive system (Figs. 1, 6, 7) consists of the testes, which vary in number from 25 to 30 and occupy the space between the digestive crura in the posterior half of the body. They are small, round or oval bodies which are not particularly regular in their arrangement, and a few of the most anterior overlap the ovary. The vas deferens (Fig. 6) is a small tube situated dorsally to the uterus. It is slightly irregular, but does not coil or fold back upon itself. The narrow tube leads directly into the cirrus, which is a small but muscular organ and opens directly into the genital pore.

The female reproductive system (Fig. 7) occupies the anterior half of the body between the digestive crura. Located about midway in the body length, lying slightly to the left, is the ovary, a rather large organ, composed of five or six large lobes which are compactly folded upon each other to give a solid appearance. It is divided into halves, the anterior portion being immature and presenting a different aspect from the posterior part, as it is darker, heavily granular, and devoid of any large ova. At the tip of this anterior part, a small lobe curves laterally and partially encloses the seminal receptacle. The posterior half is the mature portion that contains the developing ova which are large, clear and conspicuous, each one containing a large, granular, darkly staining nucleus. From this portion of the ovary,

the oviduct arises on the ventral side, crosses the ventral side of the seminal receptacle, and receives a short duct leading from the latter body, and one from the genito-intestinal canal, then passes to the ootype.

The seminal receptacle (Fig. 7) is a large, oval shaped sac, lying to the right of the ovary and is partially imbedded in the anterior end of the ovary. A short duct, leading from its anterior end, connects with the oviduct and enters the vitelline duct at the level of the genito-intestinal canal. It is a clear, almost non-staining body, with a few nuclei in the peripheral portion.

The vitellaria (Fig. 1) consist of a pair of many-lobed organs extending the full length of the body, from the point where the esophagus divides to form the digestive crura, backwards to the point where the crura fuse once more. Around the pharynx and the posterior sucking disc the regions are entirely free from vitellaria. Vitelline lobes are extremely numerous, small and closely packed, filling up each side of the body, and surrounding the digestive crura. In the live specimen the vitellaria are not apparent, but in the killed specimen (either Bouin's or Carnoy's solutions) the vitellaria show plainly. In stained mounts (either Delafield's or Ehrlich's haematoxylin) the vitellaria are so conspicuous as to obscure nearly all other structures. They have a peculiar and characteristic granular appearance caused by the presence of yolk granules, the material of which is highly refractive. The vitellaria are the last and most difficult structures to be destained, as they take the stain very heavily. Two yolk ducts leading from the vitellaria unite in the median line, anterior to the ovary, and enlarge into a conspicuous yolk reservoir. From the posterior point of the yolk reservoir the vitelline duct arises, turns abruptly to the left, joins the oviduct which receives ducts from the seminal receptacle and the genito-intestinal canal, then turns to the right, loops once, and opens into the ootype, which lies just dorsal to the yolk reservoir.

The uterus is a small (Figs. 6, 7) but rather thick-walled, ciliated tube connected directly with the ootype and leading anterior to the genital pore. Mature eggs may be seen distending the walls of the uterus, though no more than two eggs at one time have been observed there.

The vaginae (Fig. 7) are a very narrow pair of tubes arising from the anterior margins of the yolk ducts and proceeding anteriorly, close to the uterus, one tube on each side. They open at the same level as the genital pore, maintaining the same diameter throughout.

The vaginae are thus connected through the yolk ducts with the seminal receptacle and the ootype.

Briefly, the system of ducts in the reproductive system of *O. striata* is as follows: an oviduct arises from the ventral side of the posterior lobe of the ovary and turns anteriorly, receives the short duct from the anterior end of the seminal receptacle, and joins immediately with the vitelline duct which arises from the posterior point of the yolk reservoir. At this point, the genito-intestinal canal comes into the oviduct ventrally, from the left. The common duct now turns to the right, loops once, then turns anteriorly and runs dorsally to the yolk reservoir and opens into the ootype from which the uterus leads anteriorly. The vaginae connect directly with the yolk reservoir.

Mature eggs (Fig. 8) may easily be seen in the uterus. They may be obtained for study by allowing the worms to remain in a dish, and at the end of an hour or so, most of the ripe eggs will have been deposited. The egg has a chitinous, transparent shell with a polar filament at each end. At the anterior end (i.e., end deposited first) the polar filament is long and is bent rather sharply at one end, while the posterior filament is shorter and straight. There are six longitudinal ridges on the shell. The egg inside the shell is oval and full of yolk material, with a large transparent nucleus. Including the shell, the size of the egg is 500 micra by 110 micra. Exclusive of the shell the mature ovum is 230 by 90 micra.

DISCUSSION

The trematode here described is regarded as a new species in the genus *Onchocotyle* because it differs from all species of the genus previously described. The most outstanding difference is its size which appears to be smaller than any which have heretofore been reported. *O. striata* measures 4 mm to 5.5 mm in length while the form nearest in size, *O. appendiculata* (Kuhn) Van Beneden (1853) is 6 to 7 mm long. Its hooks are 1045 micra in length while those of *O. appendiculata* are 471 micra. There is thus a great discrepancy between these two species. The only other Pacific coast species is *O. somniosi* Causey (1926). The other species in the entire list of members of this genus are either European or Japanese. *O. somniosi* Causey is exceedingly large, being 17-28 mm in length; its hooks are larger and its eggs of different dimensions than those of *O. striata*. *O. somniosi* was never found on the gills of the dogfish while *O. striata* was consistently found there. The following differences were found between this form and that described by Causey (1926). Living speci-

mens of *O. somniosi* were obtained from a shark and compared with *O. striata*. A distinct difference in size, which seems to be constant, has already been mentioned. The hooks in the suckers of *O. striata* are not only smaller but have prongs of slightly different shape; they also possess a larger number of small spines on the hook. Similarly the hooks in the appendix are of a different shape and smaller than those of *O. somniosi*. The egg of the new species is smaller and has two polar filaments, whereas the egg of *O. somniosi* has only one polar filament. *O. striata* possesses 25 to 30 testes, the cirrus is small and likewise the genital atrium is small, while in *O. somniosi* the testes are up to 7 in number, the cirrus is large, and according to Causey (1926:198) there is a large atrium into which the cirrus projects. The vaginae do not become enlarged at their opening in *O. striata* as they do in *O. somniosi*. A different arrangement is present in relation to the diverticula of the digestive crura: in *O. somniosi* the lobes extend laterally in a definite and regular manner of branching, while in *O. striata* the lobes of the digestive crura extend both to the inside and outside, and their branching is very irregular. These differences in structure are sufficient to warrant the designation of this form as being entirely different from *O. somniosi*, described by Causey (1926), from a shark of the Pacific coast. *O. striata* differs from *O. spinacis* described by Goto (1894) in respect to the intestine and hooks, as well as in size. The latter form has intestinal trunks simple, no spines on hooks of suckers, and differently shaped hooks in the appendix. Similarly, the other forms described by European investigators differ from this species in several ways. Cerfontaine (1900) recounts all the species described up to 1899 and none of these correspond with the form now under question. The descriptions are not complete in all cases, but as far as can be ascertained from the material available, unquestionably *O. striata* should be designated as a new species.

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PLATE 14

<i>a</i> - appendix	<i>i</i> - intestine
<i>ab</i> - appendix branch (digestive system)	<i>o</i> - ovary
<i>ao</i> - anterior lobe of ovary	<i>od</i> - oviduct
<i>as</i> - anterior sucker	<i>ol</i> - ootype
<i>at</i> - anterior terminal (excretory system)	<i>p</i> - pharynx
<i>c</i> - cirrus	<i>po</i> - posterior lobe of ovary
<i>db</i> - disc branch (digestive system)	<i>s</i> - sucker
<i>dc</i> - digestive crus	<i>sd</i> - sucking disc
<i>dl</i> - dorsal lip of sucker	<i>sr</i> - seminal receptacle
<i>e</i> - esophagus	<i>t</i> - testes
<i>ec</i> - excretory canal	<i>u</i> - uterus
<i>ed</i> - esophageal diverticulum	<i>va</i> - vagina
<i>ep</i> - excretory pore	<i>vd</i> - vitelline duct
<i>gi</i> - genito-intestinal canal	<i>vi</i> - vitellaria
<i>gp</i> - genital pore	<i>vp</i> - vaginal pore
<i>h</i> - hook	<i>vr</i> - vitelline reservoir
	<i>vs</i> - vas deferens

Fig. 1. Ventral view of entire worm. $\times 25$

Fig. 2. Hook from sucker of sucking disc. $\times 55$

Fig. 3. Hooks from appendix. $\times 250$

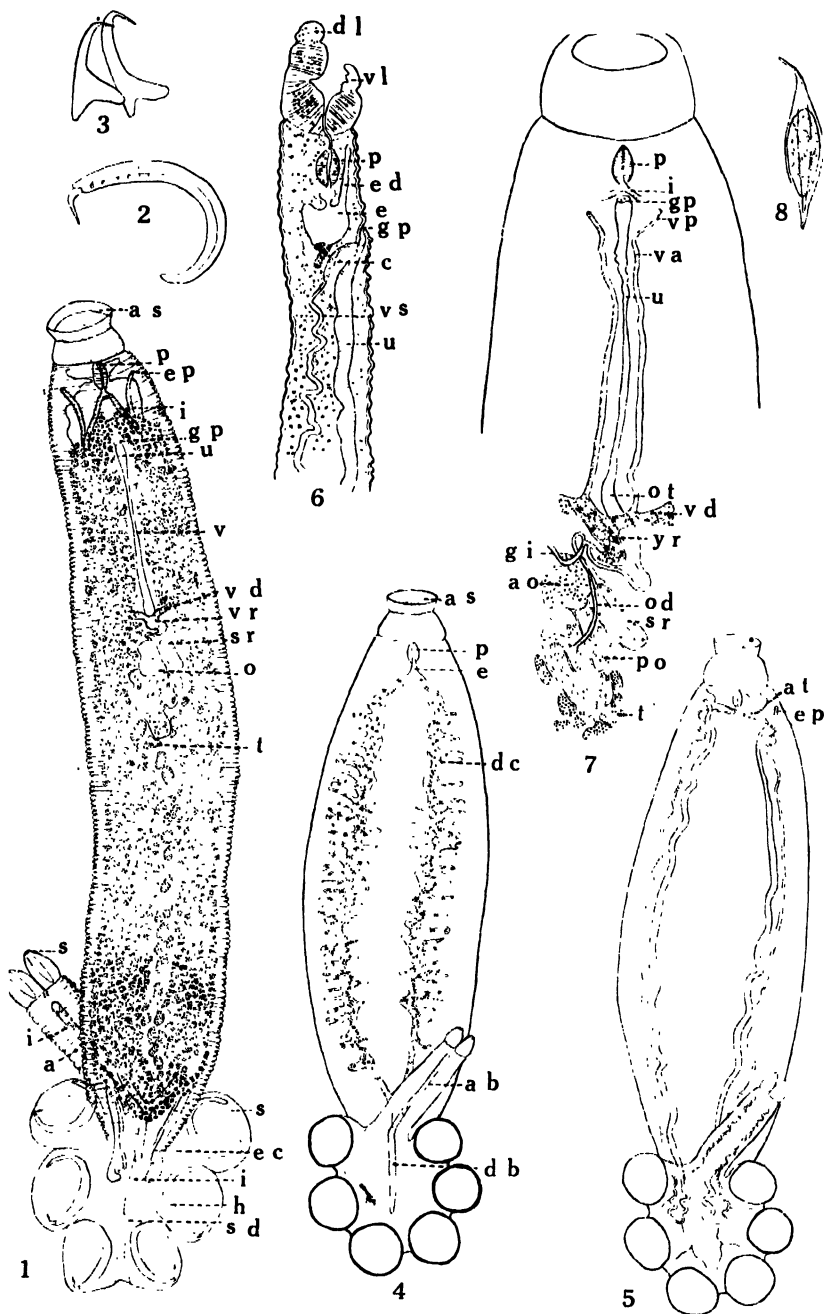
Fig. 4. Digestive system, dorsal view, living specimen. $\times 23$.

Fig. 5. Excretory system, dorsal view, living specimen. $\times 23$

Fig. 6. Median sagittal section through anterior end showing mouth regions and reproductive system. $\times 51.5$

Fig. 7. Schematic view of female reproductive system, ventral view. $\times 55$

Fig. 8. Mature egg, as laid in dish. $\times 52$



Tissues Involved in the Transfer of Mineral Salts in Plants

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INTRODUCTION

The study of the paths of transfer of mineral salts in plants is a subject of especial interest from the standpoint that while much has been written on it little evidence has been offered in the form of published data. The data reported in this paper are an attempt to furnish experimental evidence concerning the movement of mineral salts in woody plants.

The work was undertaken at the suggestion of Dr. E. N. Transeau, and was carried on at Ohio State University during the winter of 1925 and the spring of 1926.

It is well to review briefly at this point what is known concerning the movement of mineral salts in plants. In the early part of the eighteenth century Stephen Hales (1727) established the fact that the ascending stream of water is carried by the wood. In dealing with physiological problems Hales used the earlier anatomical studies of Grew (1682) as a foundation.

De la Baissè (1733) placed cut ends of branches in colored fluids and found that the general body of the wood and the woody bundles which pass from it were colored. The succulent parts of the bark and leaves remained uncolored, showing that the red juice had passed through the wood. Such experiments show that the dyes follow the path of the absorbed water but this is no proof that mineral salts in solution follow the same paths.

Writings of the plant physiologists of the nineteenth century show that they recognized the function of the wood in conveying mineral salts in solution. Sachs (1882) concludes that salts in dilute solution (1:2000 or less) are carried in the ascending stream of water in the wood cell-walls. These ideas were obtained as a result of experiments with lithium nitrate. Other writers make statements to the effect that the salts are carried up in dilute solution through the wood in the transpiration stream. Strasburger (1908) states in effect that the nutrient salts are conveyed in plants by the transpiration current. Jost and Pfeffer make similar statements in their textbooks of plant physiology. Early investigations were

made not so much to determine the path of transfer of salts as to study the movement of the transpiration stream itself.

Recent experiments by Curtis (1920, 1923, 1925) upon the transfer of nitrogen and ash constituents through woody plants have furnished data not in accord with earlier ideas. On the basis of his data Curtis concludes that salts, chiefly nitrates, may be transferred through the phloem elements. Since the xylem has heretofore been considered as the path of movement of mineral salts, occasion has arisen for the experiments by the writer.

Consideration of the mechanism of transport in plant tissues is of importance, since no definite conclusion can be reached as to which tissue is the path of transfer of some particular substance without some notion as to how this transfer may be taking place. It is also essential to understand the respective abilities of xylem and phloem elements for conducting mineral salts in the quantities and at the rates at which they are known to be transported in woody plants.

Diffusion may take place through both of the tissues. However this method is ruled out as too slow a process to account for known movements of salts in plants.

De Vries (1885) states that streaming and rotating of the protoplasm is common in the xylem and phloem elements of woody plants. He concludes that this movement might serve as an agency for transfer of material through plants, stating that the movement of water as well as of nutrient substances takes place by this method.

Another theory is that the transfer from cell to cell occurs along threads of protoplasm. If we know that continuity as conditioned by life processes is maintained by the thinnest threads, the thick coarse connexions may readily be supposed to perform important conducting functions. Pfeffer (1906) mentions such a possibility. More recently Kidd (1917) speaks of translocation as being continuous through the connecting threads of protoplasm.

The most widely accepted theory is that the mineral salts, after being absorbed in solution by the roots, pass into the transpiration stream and are carried upward. Their writings show that this opinion was held by Sachs, Jost, Pfeffer and Strasburger. Since the time of these men, quite a number of investigators have attempted to correlate the transpiration of plants with salt absorption. Due to different conditions under which the experiments have been carried out and the different methods of interpreting the data, opinions are divided as to the role of transpiration in affecting the movement

of salts. One sees, however, that a consideration of water loss is an important item when one attempts to study the tissues involved in the transfer of mineral salts in woody plants.

It is not intended to imply that a complete division of labor exists such that the xylem conveys only one kind of material and the phloem another. The proximity of the two tissues and the nature of their cells permit cross transfer. Once this has occurred, there is no opposition to translocation, particularly in the case of mineral salts, within either or both of the tissues.

MATERIAL

Plants used in experiments such as these must show a range of conditions and must be well adapted for such experiments. They should be hardy, rapidly growing and allow a ready separation of the xylem and phloem elements. Care was taken to use only well-rooted plants. Those with injured roots were avoided.

Salix amygdaloides, *S. nigra*, *S. fragilis*, *Liquidamber styraciflua* and *Acer negundo* are well adapted to use in such experiments. *Salix* was found to be of value in certain types of experiments because of the ease with which root growth may be obtained on different portions of the stem.

Salts used in the tests were the nitrates of lithium and caesium; the nitrates were preferred because they are less toxic.

HISTORICAL

The first record of a similar use of the salts mentioned is that of McNab (1871, 1874) who used lithium and caesium. Pfitzer (1877) used salts of lithium and thallium. Sachs (1878) used lithium nitrate for testing the rapidity of water transfer in transpiring plants. He found the lithium to move at the rate of 2.1 meters per hour in rapidly transpiring plants. In this work 1-2 per cent solutions were used. All the uses made of these salts were to determine the rapidity of water transfer in transpiring plants.

Curtis (1923) has objected to the use of salts of lithium and iron on the basis of their toxicity, and to lithium further for the ease with which it penetrates membranes. He mentions that studies in the past have indicated a movement and an accumulation of salts in the xylem.

Voelcker (1900-1915) used lithium salts in his pot cultures with wheat. Amounts equivalent to 0.003 per cent of the metal were

found to cause decreased yield and to retard germination; lesser amounts stimulated growth. It is to be expected, however, that amounts considerably in excess of these could be used in tissue studies of short duration without toxic effect sufficient to introduce any appreciable error. In the same group of experiments Voelcker found caesium salts much less toxic than those of lithium.

Lucannus (1865) grew plants of *Vicia sativa* in solutions of lithium, caesium and rubidium to test the replacement of the potassium ion. No ill effects were noticed until the time of blooming. These were attributed by Lucannus to the lack of chlorides in the culture solutions.

METHODS

The plants were always tested in the same medium in which they were growing; thus if growing in culture solutions, the salt was added to the solutions; if growing in pots or trays, the solution was poured about the base of the plant.

Salts of lithium and caesium offer the advantage that they do not commonly occur in plants and that they can be readily detected in plant tissues. The tests are made by burning a bit of leaf or stem in the Bunsen flame and viewing the flame through the spectroscope. Lithium is easily recognized by the scarlet, and caesium by the blue lines imparted to the spectrum. Since caesium is much less toxic to plants and also has a much slower rate of entrance, it appears to be well adapted to checking results obtained with lithium salts.

The method used in removing tissues were similar to those employed by Curtis (1920, 1923, 1925) in his studies on the transfer of nitrogen and ash constituents in certain woody plants.

In the first experiments sections of phloem tissue were removed from the stems by peeling sections of the bark 1-2 cm in length. The wounds were scraped to remove adhering strands of cambium and to prevent the growth of new phloem element. A thin coating of paraffin of melting point 40-50° C was applied at once to prevent drying and infection of the remaining tissues.

In almost all cases the plants lived and showed little if any ill effects after the removal of the phloem tissue. The same was true after the removal of the xylem in the manner described later. However a decrease in transpiration was noted in the plant parts above the rings. Such decreased transpiration may have been due to the blocking of the tracheae by air bubbles, or by substances produced

by changes of decay in the cambium and exuded into them from the cut ends of the cambium above and below the ring. Such a blocking has been suggested by Dixon (1922) and would hinder the passage of both water and mineral salts past a ring.

This makes advisable a method whereby the xylem as well as the phloem is removed. A direct comparison can thus be made of the movement of salts from the roots into the foliage parts through ringed stems, or stems from which the sections of the xylem have been removed.

Removal of the xylem sections destroyed water conducting tissue and necessitated the supplying of water to the upper parts of the plants. This was accomplished by fastening glass tubes 10-12 cm in length about the plant stems by means of rubber stoppers. When these tubes were filled with water the cut was prevented from drying out and water was supplied to the top of the plant. Experiments using split twigs with the idea of having the water supplied through one side while the xylem was removed from the other did not prove satisfactory. Most of the plants died when they were subjected to this type of treatment.

MOVEMENT OF LITHIUM SALTS WHEN XYLEM OR PHLOEM IS CUT

Phloem cut in Salix. These experiments were conducted with 40 specimens of *Salix amygdaloides* and *S. nigra*. Twenty specimens were ringed to remove the phloem and the remaining 20 were used as checks. Plants used as checks were about the same size as the test plants and in close proximity to them. All the plants, well-rooted cuttings, had been grown in sand in a green house and were tested in this soil. The ringing was done on March 29 and a 1 per cent solution of lithium nitrate was added to the base of the plants. At the same time a solution of calcium carbonate was added to the sand to reduce any toxic effects which might be exerted by the lithium salt. Tests were made for lithium by the method previously described. The movement of the salt into the upper parts of the plants is shown in table 1.

The data show that cutting the phloem results in a retardation of the movement of lithium compared with the rate of movement through normal stems. As the experiment was allowed to continue, a movement was noted past the rings showing that while ringing a transpiring stem retards the rate of movement of salts, it does not result in a complete obstruction to the movement into the parts above the ring.

TABLE 1. *Effect of the cutting of the phloem on movement of lithium through Salix*

Date of test	Positive test in checks	Positive test in samples
April 3.....	14	0
April 5.....	15	1
April 7.....	19	2
April 9.....	20	2
April 12.....	20	5
April 30.....	20	19

Xylem cut in Salix. Since experiments in which the phloem tissue was cut by ringing showed that a movement of lithium may take place past a ring, it seemed profitable to determine whether such a movement could be obtained past a cut removing a section of xylem. Fourteen specimens of *Salix nigra* growing in sand were used for this purpose. The xylem was cut in 7 of the specimens on April 10 and a 1 per cent solution of lithium nitrate was poured about the base of the samples and checks. Table 2 shows the results of tests for lithium.

TABLE 2. *Effect of cutting the xylem on movement of lithium through Salix.*

Date of test	Positive test in checks	Positive test in samples
April 11.....	7	0
April 13.....	7	0
April 17.....	7	0
April 20.....	7	0
April 26.....	7	0

The indication is that while removal of a section of phloem causes a retardation of the movement of lithium, the removal of xylem sections completely obstructs such movement in the length of time involved.

Since no tests for lithium were obtained in the leaves of the plants, it seemed of interest to ascertain to what distance, if any, the salt might have moved upward due to agencies of transport other than the transpiration stream. Such an agency as diffusion would

not be affected by the cutting of the xylem in the way that the transpiration stream would.

Three of the specimens were examined on May 1. The phloem and xylem tissues were removed and each tested for traces of lithium. In one sample the lithium had moved upward only 6.3 cm above the surface of the sand; in the main stem of another sample it had reached a height of 13.9 cm, but in a side branch which left the main stem 10.2 cm above the sand, the salt had ascended to the tip of the branch. In the third sample no positive test was obtained in the main stem above a height of 6.3 cm, but in a side branch leaving the main stem at a distance of 2.5 cm above the sand, the salt had risen 50 cm to the top of the branch.

Evidently the presence of a transpiring part of the plant above that part into which the salt had moved accounted for the rapid upward movement in the side branches in which the xylem was left intact.

A sample tested on May 29, showed positive lithium lines. Tests were obtained in the leaves as well as in the phloem and xylem tissues. However upon sectioning the stem, where the cut had been made to remove the xylem, and applying the lignin test (hydrochloric acid and alcoholic phloroglucin), it was found that new xylem tissue had been laid down, evidently by cambium not removed when the cut was made. This then lends further support to the idea that the mineral salts are transported in the xylem.

Phloem or xylem cut in Salix. To further check the work already done, well rooted cuttings of *Salix fragilis* were used in another series of experiments. The cuttings were placed in jars containing 0.2 per cent solutions of lithium nitrate to which small amounts of calcium carbonate had been added. Each set of specimens consisted of one specimen from which the xylem had been removed, another which had been ringed, and a third specimen used as a check. The specimens were placed in the lithium solutions on April 17 and tested at intervals of two or three days until May 14. Only a part of the results are recorded in table 3, since results of all sets were similar.

TABLE 3. *Effect of the cutting of the xylem and of the phloem on the movement of lithium through Salix fragilis*

Set	Phloem cut	Xylem cut	Check
A.	Positive test 15.2 cm above cut	Negative test 15.2 cm above cut	Positive test in all leaves
B.	Positive test 10.1 cm above cut	Negative test 7.6 cm above cut	"
C.	Positive test 20.2 cm above cut	Negative test 12.7 cm above cut	"
E.	Positive test 27.8 cm above cut	Negative test 12.7 cm above cut	"

These results show clearly that a movement of lithium occurs past a ring but that the salt in the time allotted fails to pass a cut removing a section of xylem.

In order to determine whether any diffusion was taking place from the unsealed ends of the cut xylem into the distilled water in the tubes, this water was tested for lithium. The water was carefully evaporated, the dish moistened with hydrochloric acid and the usual test applied. All tests showed negative results.

Specimens with xylem sections removed were allowed to stand until May 14 but still showed negative tests at this date.

Phloem or xylem cut in other plants. In the next experiments the movement of lithium salts through *Liquidamber styraciflua* was investigated. The specimens used were 30-90 cm seedlings growing in a green house. The same methods were employed as in the preceding series. One tenth per cent solutions of lithium nitrate were added to the roots of the plants after the removal of sections of xylem and phloem. A retarded movement was noted past rings removing the phloem tissue. No movement was detected past a cut removing xylem tissue.

At the same time experiments were run to test the transfer of mineral salts through the stems of 30-90 cm seedlings of *Acer negundo*. The movement of the salt was found to be more rapid than in the case of *Liquidamber*, but again the failure of the lithium to pass a cut removing a section of xylem was evident. A retarded movement was noted through ringed stems.

MOVEMENT OF CAESIUM SALTS WHEN XYLEM OR PHLOEM IS CUT

Lithium salts have been used in all of the preceding experiments as a means of testing mineral salt transfer. Salts of caesium possess less power of penetration into plants. They are also less toxic than lithium salts. Therefore they are ideal for use in testing the transfer of mineral salts and especially valuable for checking results obtained with lithium. Caesium may likewise be detected in minute quantities by the spectroscopic method. It is recognized by the twin blue lines, Caesium α and Caesium β .

On May 24 specimens of *Salix fragilis* as in table 3 were placed in 0.5 per cent solutions of caesium nitrate. Five days later all checks showed strong caesium tests. Ringed specimens likewise gave strong positive tests, but specimens having sections of xylem removed from their stems gave negative tests in all cases. These latter specimens gave negative tests until June 24 when the experiment was discontinued. The indication is that caesium salts do not pass a cut in the xylem tissue.

Transfer of caesium was also tested through *Liquidamber styraciflua* and *Acer negundo*. All results were entirely in accord with those previously obtained with lithium. The specimens used were 30-90 cm seedlings growing in a green house. After removal of the sections of tissue 1 per cent solutions of caesium nitrate were added to the roots of the plants. The tests were made in the usual manner.

EFFECT OF TRANSPIRATION ON THE MOVEMENT OF MINERAL SALTS

The movement of water upward in plants in the "transpiration stream" is assumed to take place principally in the xylem elements. Since such a movement would obviously aid in mineral salt transfer, it is of importance to note whether any correlation exists between the rate of transpiration and the rate of transfer of the mineral salts. Sachs (1882), Pfeffer (1906) and Jost (1903) state that a "transpiration current" is necessary to supply adequate quantities of the essential salts to plants.

Experimenters have attempted to correlate rate of transpiration with the variation of the ash content of plants. Hasselbring (1914) in working with tobacco plants in Cuba, found that the plants transpiring the least, often had the greater ash contents. Muenscher (1922) found a slight reduction of ash content of pure line barley plants upon decrease of transpiration. After a series of careful experiments Auchter (1923) decided that the amounts of ash found

in stems can not be used as criteria for the absorption or translocation of water or of nitrates. Pràt (1923) employed an electrolytic method to measure the effect of transpiration rate on ion absorption. Absorption of ions continued rapidly with low transpiration, but in all cases plants in dry air and having the greatest transpiration rates absorbed the greatest number of ions. Dixon and Atkins (1915) found a decrease in concentration of electrolytes from the wood of roots upward to the stems. They say, "This would seem to suggest that while the quantity of dissolved carbohydrates in the transpiration stream may be added to on its upward passage, the amount of dissolved electrolytes is not thus reinforced but usually is diminished as the stream rises."

The following experiments were attempted to determine how the practical elimination of transpiration would affect the movement of mineral salts in woody plants.

Specimens of *Salix fragilis* with glass receptacles fastened about the stems were placed in dilute solutions of lithium nitrate. By filling the receptacles with water all of the transpiring parts were immersed. At the end of 18 hours all the checks not immersed in water showed the usual tests. No positive tests were obtained in the leaves of samples. An examination of the xylem and phloem tissues of the stems showed lithium present at the height of one inch above the roots. A movement so slight may be accounted for solely on the basis of diffusion. Hence we must assume that the practical elimination of transpiration seriously retards the upward movement of mineral salts.

Another series of experiments was set up on April 24. The under surfaces of the leaves of specimens of *Salix fragilis* were coated with vaseline in order to reduce transpiration. These plants, with the checks, were tested beside plants whose transpiring parts were immersed in water in the manner described above. At the end of 50 hours lithium was detected at the height of 29 cm in the specimens whose leaves had been coated with vaseline. In those plants having their foliage parts immersed in water the salt had reached an average of only 5 cm.

DOWNWARD TRANSFER OF MINERAL SALTS

In all previous experiments by this writer only the upward transfer of salts has been considered. If we assume that the xylem is the path of upward transfer, the question arises as to which tissue would serve to conduct these same salts downward.

Glass tubes were attached to the upper parts of the stems of *Salix nigra* and *S. fragilis*. These tubes were then kept filled with water. When good root growth had been obtained at the tops of the stems, sections of xylem and phloem were removed from the stems below and dilute solutions of lithium nitrate used to replace the water in the tubes above. The leaves of check stems showed strong lithium tests at the end of a few hours. Plants ringed below the tubes required 24-36 hours before showing lithium tests. This constituted a movement of 8-12 cm in most cases. Those plants from which 1-2 cm sections of xylem had been removed showed no tests for lithium at the end of 7 days, the duration of the experiment.

While the number of experiments run was not sufficient to furnish conclusive data, the indication is that mineral salts are carried downward in the xylem tissue.

Dixon (1922) speaks of the xylem as the path of a downward moving stream. This stream is explained on the basis that there is a tension set up by the transpiration of other parts of the plant. This sets up a downward moving current in which the mineral salts are carried.

DISCUSSION

Quite a number of ringing experiments have been reported, the purpose of which has been to determine the paths followed by solutes in woody plants. Up to the present time few experiments have been reported in which both xylem and phloem tissues have been removed in testing for the transfer of salts. The objection raised to experiments in which only one tissue has been cut is that the cutting of that tissue might seriously alter the conducting power of the entire stem. It appears that when both tissues are cut in respective plants this objection is removed, since with all other conditions the same, the chances for changes in the conducting systems of each plant are equally great.

Xylem and phloem tissues both appear to be well adapted for the transport of solutes. The exact nature of this transfer is unknown at present though numerous suggestions have been made. There is obviously some connection existing between the upward transport of solutes and the transpiration of the plant. The upward moving mass of water certainly provides an excellent medium by which soluble materials might move. It has long been known that the "transpiration stream" is the movement upward of a dilute solution of soluble materials including the mineral salts.

Experiments performed by the writer indicate that the xylem is the path of transfer of mineral salts, any movement of these through the phloem being negligible. There is evidence that a movement may take place independently of transpiration but that increased transpiration results in increased absorption and rate of movement.

SUMMARY AND CONCLUSIONS

Experiments reported in this paper were performed on species of *Salix*, *Liquidambar* and *Acer*; conclusions must be considered as drawn only for those particular species used and for the particular salts of lithium and caesium used.

Xylem and phloem tissues were cut in respective plants and precautions taken to prevent injury or drying of the remaining tissues. Low concentrations of salts were used to avoid toxic effects. Lithium and caesium possess the advantage of being easily detected spectroscopically in plant tissues and do not occur as normal constituents.

Removal of a section of phloem by ringing retards the movement of lithium and caesium into the plant parts above the ring. This may be due entirely to lessened transpiration noted in the case of ringed plants.

Removal of a 1-2 cm section of xylem results in completely obstructing the upward movement of salts of lithium and caesium. In one case in which a positive test was obtained new xylem tissue was found to have developed.

Reducing the transpiration results in a much reduced rate of movement of salts upward. The practical elimination of the transpiration factor decreases the movement to the point where diffusion alone might be considered to account for the transfer.

Studies on the downward transfer of mineral salts indicate that such a movement may occur through the xylem.

It seems that the upward and downward movement of mineral salts occur principally through the xylem tissues and that the chief agent by which this movement takes place is the transpiration stream, though the movement may be aided by diffusion, by protoplasmic streaming, or by transfer along threads of protoplasm.

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Orthopagurus, a New Genus of Paguridae From the Pacific Coast

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The description of *Pylopagurus schmitti* Stevens, a new species as recorded in Publications Puget Sound Biological Station (3: 297-299, figs. 19-22. 1925), is based on male specimens only; the female was not found up to that time.

During the summer of 1925, a biological survey under the direction of Dr. John E. Guberlet of the University of Washington was undertaken in the vicinity of the Puget Sound Biological Station, Friday Harbor, Washington. Rather extensive dredging was done. While assisting with the survey, numerous specimens of *Pylopagurus schmitti*, both male and female, were collected by the writer. Examination of the material thus obtained and further investigation revealed characteristics such as to exclude this form from the genus *Pylopagurus* Milne-Edwards and Bouvier, and to prevent its reversion to the genus *Pagurus* Fabricius, as at present known.

Dr. Waldo L. Schmitt has called the writer's attention to the fact that *Pylopagurus minimus* (Holmes), which as yet has not been found in the Friday Harbor region, exhibits generic characteristics similar to those of *Pylopagurus schmitti* Stevens. *Orthopagurus* is now proposed as a new genus to include these two forms. The key to the genera of the hermit crabs of Friday Harbor, Washington, as given in the above mentioned reference, is accordingly revised. The distinguishing character used by certain authors, based on the fingers of the chelipeds opening and closing horizontally or obliquely is disregarded in the present paper for it has been found very indefinite, particularly as a means of separating the juvenile specimens.

The marine worms whose tubes are inhabited by *Orthopagurus schmitti* were identified by Dr. A. L. Treadwell of Vassar College.

In addition to the literature listed in the brief synonymy under each species the paper which has been most helpful in the preparation of this article is:

Alcock, Catalogue of Indian Decapod Crustacea; Pagurides; Part 2, fasc. 1, pp. 11-197, pls. 1-16, Indian Museum, Calcutta, 1905.

Acknowledgements are due to Professor Trevor Kincaid, Dr. T. C. Frye and Dr. John E. Guberlet of the University of Washington and to Dr. Waldo L. Schmitt of Smithsonian Institution for valuable advice and the loan of various specimens.

KEY TO THE GENERA OF THE PAGURIDAE OF THE
FRIDAY HARBOR REGION

- A. Chelipeds similar and equal, subequal or one (usually the left) larger than the other; external maxillipeds approximated at base; abdomen with paired appendages on first two segments of male, and on first segment of female; gills 13 on either side. PAGURISTES, p. 247.
- AA. Chelipeds dissimilar and unequal, the right much the larger; external maxillipeds widely separated at base; abdomen with no paired appendages on first or second segments of either sex: gills 11 on either side.
- B. Abdomen spirally coiled; telson and uropods not symmetrical, usually better developed on the left side than on the right. PAGURUS, p. 247.
- BB. Abdomen not spirally coiled but flexed; telson and uropods symmetrical. ORTHOPAGURUS, p. 247.

Comparison of the Genera	Paguristes	Pagurus	Orthopagurus
Chelipeds similar.....	+	—	—
Chelipeds equal or subequal.....	+	—	—
Right cheliped usually much the larger when the two are unequal.....	—	+	+
Fourth pair of legs simple.....	+	—	—
Fourth pair of legs subchelate.....	—	+	+
External maxillipeds approximated at base.....	+	—	—
External maxillipeds widely separated at base.....	—	+	+
Abdomen with paired appendages other than the uropods.....	+	—	—
Number of gills on either side.....	13	11	11
Abdomen spirally coiled.....	+	+	—
Abdomen merely flexed.....	—	—	+
Telson and uropods symmetrical.....	—	—	+
Telson and uropods asymmetrical, usually better developed on the left side.....	+	+	—

Genus *PAGURISTES* Dana

Chelipeds similar and equal, subequal or one (usually the left) larger than the other. Fourth pair of legs simple. External maxillipeds approximated at base; exopodites of all three pairs of maxillipeds flagellate. Abdomen spirally coiled, with paired appendages other than the uropods; paired appendages on the first two segments of the male and on the first segment of the female. Telson and uropods better developed on the left side than on the right. Gills phyllobranchiae, 13 on either side.

Genus *PAGURUS* Fabricius

Chelipeds usually dissimilar and unequal, the right much the larger; very rarely subequal (not so in Friday Harbor species). Fourth pair of legs subchelate. External maxillipeds widely separated at base; exopodites of all three pairs of maxillipeds flagellate. Abdomen spirally coiled, with no paired appendages except the uropods in either sex. Telson and uropods usually better developed on the left side than on the right. Gills phyllobranchiae, 11 on either side.

Genus *ORTHOPAGURUS*, new genus

Chelipeds dissimilar and unequal, the right much the larger. Fourth pair of legs subchelate. External maxillipeds widely separated at base; exopodites of all three pairs of maxillipeds flagellate. Abdomen not spirally coiled but flexed, with no paired appendages except the uropods in either sex. Telson and uropods very nearly symmetrical. Gills phyllobranchiae, 11 on either side.

Key to the Species of Orthopagurus

- A. Large hand distally widened, base narrow and convex, distal portion declivate with edges upturned; lateral teeth of front rounded. *O. minimus*, p. 247.
- AA. Large hand nearly uniform in width, flattened or slightly convex; lateral teeth practically obsolete. *O. schmitti*, p. 249.

ORTHOPAGURUS MINIMUS (Holmes)

Pagurus minimus Holmes, Occas. Papers Calif. Acad. Sci. 7: 145, 1900; Rathbun, Harriman Alaska Exped. 10: 160, 1904.

Pylopagurus minimus Schmitt, Univ. of Calif. Pub. in Zool. 23: 144, Pl. 16, figs. 1a, 1b, and 1c, 1921.

Characters.—Somewhat pubescent. Anterior portion of cara-

pace about as wide as long; median tooth of front triangular, acute; lateral teeth rounded. Eye stalks stout, cylindrical, a little flattened distally, about two-thirds the length of the anterior portion of the carapace. Antennal acicle not reaching the tip of the eye. Large cheliped with merus compressed; carpus distally widened, upper surface rounded and armed with short spines which incine forwards; hand oblong, widening distally to a short distance beyond the base of the movable finger; base convex, armed with anteriorly inclined spines; distal portion declivate and practically spineless except along the outer margin of the fingers; fixed finger broad; outer edge evenly rounded, sharp, upturned, armed with anteriorly inclined spines; the upper surface smooth and concave; movable finger broad, widest a little beyond its articulation; outer margin sharp, spiny, evenly curved; upper surface nearly smooth and concave; inner margin of both fingers with large, white, tubercular teeth. Smaller cheliped narrow, much shorter than the larger; hand rounded, the upper surface oblique; fingers longer than the palm. Ambulatory legs



Fig. 1. *Orthopagurus minimus* (Holmes), female, $\times 3.3$.

rather slender, laterally compressed, pubescent; dactyls slender, curved, tapering from the base, spiny below and slightly longer than the propodi.

Color.—General color reddish, with spots of darker red, larger cheliped a darker red than the rest of the body, especially at the distal end; ocular peduncles with a median, transverse, light colored band (Holmes).

General Distribution.—Skidegate, Queen Charlotte Sound, British Columbia; San Francisco, Monterey Bay, Laguna Beach and San Diego, California, 27.4 to 64 meters (Schmitt).

Local Distribution.—Not found in the Friday Harbor region.

Remarks.—A specimen of *Orthopagurus minimus* from Monterey Bay, California, and also one from Skidegate, Queen Charlotte Sound, British Columbia, loaned by the Division of Invertebrates of the Smithsonian Institution, were examined. It has been found in worm tubes (Benedict) and in Dentalium ("tooth") shells between the Farallones and the Golden Gate (Schmitt).

ORTHOPAGURUS SCHMITTI (Stevens)

Pylopagurus schmitti Stevens, Publ. Puget Sound Biol. Sta. 3: 297-299, figs. 19, 20, 21 and 22, 1925.

Characters.—Somewhat pubescent, particularly on the chelipeds. Anterior portion of carapace little longer than wide; median tooth of front triangular, acute, prominent; lateral teeth practically obsolete. Eye stalks stout at base but rather tapering, about two-thirds the length of the anterior portion of the carapace. Antennal acicle not reaching the tip of the eye. Large cheliped with merus compressed; carpus distally widened, upper surface rounded and armed particularly along inner surface with spines which incline forward; hand oblong, of nearly uniform width; inner margin of palm armed with spines similar to those of the carpus, upper surface slightly convex but appearing quite flattened; fixed finger broad, its outer edge with small anteriorly inclined spines; movable finger more nearly uniform in width. Smaller cheliped rather stout, nearly as long as the larger; hand somewhat flattened; fingers about same length as the palm. Ambulatory legs rather slender, laterally compressed, pubescent; dactyls slender, curved, decidedly tapering from the base, spiny below, about the same length as the propodi.

Color.—Pale pinkish buff to white with irregular spots and

bands of orange cinnamon; the fingers being tipped with apricot orange; the fingers of the large hand are armed on the inner margins with large white, tubercular teeth; antennae orange vinaceous.

Local Distribution.—Common west off Reed Rock at 70 meters. Rather numerous northwest off Brown Island at 6 to 10 meters and between Brown Island and Reed Rock at 50 to 100 meters; off Point Caution, San Juan Island at 22 to 37 meters; off Minnesota Reef at 80 meters; northeast of Turn Rock at 160 meters; both north and south of Flat Point, Lopez Island at 20 to 60 meters and in Griffin Bay near Cattle Point, San Juan Island at 77 meters. Collected also north of Orcas Island at 12 to 14 meters; south of Johnson Point, Sucia Island, at 14 to 40 meters; between Mattia Island and Puffin Island at 24 to 26 meters; northwest of Jones Island at 220 meters.



Fig. 2. *Orthopagurus schmitti* (Stevens), female, $\times 3.5$.

Remarks.—The type, a male, taken at about 37 meters off Point Caution, measures 34 mm. in length and is deposited with the Division of Marine Invertebrates of the Smithsonian Institution.

O. schmitti is best distinguished from *O. minimus* by the characteristics of the large hand, which in *O. schmitti* is nearly uniform in width and appears flattened above, while in *O. minimus* it is distally widened and has the distal portion declivate with the edges upturned. The upper surface of the large hand of *O. schmitti* varies greatly both in length and in degree of convexity; in juvenile specimens it is shorter in proportion to the width than in older individuals, and appears nearly flat, while in the latter it is in most cases easily seen to be convex.

O. schmitti has been found in the tubes of the marine worms, *Sabellaria cementarium* Moore and *Serpula* sp. but more commonly in the former. The fact that the tubes are usually attached may account for the comparatively small number of specimens which have come up in the dredge even tho the local range is large. This idea is further substantiated by the fact that they have been rather com-

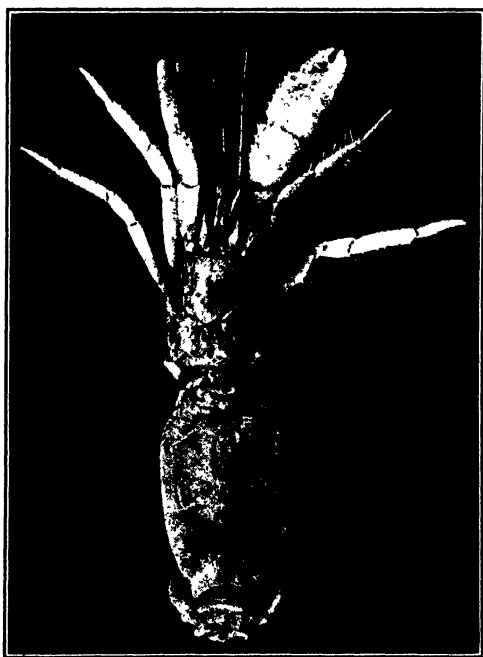


Fig. 3. *Orthopagurus schmitti* (Stevens), male, $\times 3.5$.

monly found inhabiting worm tubes attached to the rocks which have been pulled up with kelp holdfasts off the northwest shore of Brown Island, near the town of Friday Harbor, Washington.

As this paper goes to press a manuscript by M. W. de Laubenfels is received to appear in Publ. Puget Sound Biol. Sta. Vol. 5. In this is described a species of sponge with which the worm tubes inhabited by *O. schmitti* are often associated.



Fig. 4. *Orthopagurus schmitti* (Stevens) in tube of *Sabellaria cementarium* Moore, $\times 1.5$.

Experiments on Conduction in *Nereocystis luetkeana*

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The data reported in this paper are the result of an investigation to determine whether there is a translocation of water and mineral salts from one part of the plant to another comparable to known movements in higher plants.

The work was done at the Puget Sound Biological Station at Friday Harbor, Washington between July 11 and August 10, 1927.

PLANT

The bladder kelp (*Nereocystis luetkeana*) consists of a slender stipe attached by a powerful holdfast and enlarging at the top into a hollow pneumatocyst which bears the fronds at the surface of the water. The pneumatocyst may reach several meters in length and terminates in a bulb-like float. Its inner surface is covered by the cobwebby mass of sieve-tubes; these not only line the pneumatocyst, but extend up into the central portion of the fronds.

The gross anatomy of the plant suggests that translocation of materials might take place from the fronds to other parts of the plant by way of the sieve-tubes. The structure of the stipe, however, is such that it seems to be perfectly capable of manufacturing its own food materials and absorbing such salts as it might need from the surrounding water. The hapteres of the holdfast alone appear to be less well adapted to these functions.

Attention was not confined to the sieve-tubes, but the effort was made to determine whether any paths of conduction are present such as are found in the higher plants.

MATERIAL

Fresh material was used throughout the investigation. The plants used in the first series of experiments were 10 to 20 meters in length. These were growing in the kelp bed off Brown Island and were allowed to remain in that situation while the tests were being made.

Plants used in the second series were much smaller specimens. These were 1 meter or less in length but all had well developed sieve-tubes. They were collected in the vicinity of the Biological Station

and were brought into the laboratory where they were kept in running sea water during the course of the investigation. About 25 plants in all were used.

Solutions of lithium and similar salts have been used by investigators, including the writer, to detect the paths of transfer in higher plants. Because of its adaptability to the type of experiments used and particularly because of the ease with which it may be detected by the spectroscopic method, use was made of lithium chloride.

METHOD 1

In the first experiments the attempt was made to introduce the solutions into the plants by means of a hypodermic syringe. 1% and later 5% solutions were introduced at the base of the fronds. Injection was found to be very difficult because of the mucilaginous nature of the plants.

The plants were collected and brought into the laboratory at intervals of 12, 24, 36 and 48 hours after the injections had been made. After the material had been dried, tests were made for the presence of lithium by burning and viewing the flame with the spectroscope. All tests denoted the complete absence of the salt even when the tests were made at the points where the injections had been made. These negative tests may have been due to the failure actually to introduce any of the solution.

Injections were made into the fronds of other plants growing in the same situation; the same strengths of solution were used as in the above. In this case sufficient pressure was exerted with the syringe to cause swellings which were then filled with the solution. This made it certain that some of the solution actually entered the plants.

However, when the plants were brought in and tested as before, lithium was found to be absent in all parts. Check plants were injected in the same manner and then thoroughly washed in running sea water; when these were immediately dried and tested, strong tests were obtained showing the presence of lithium. This led to the conclusion that the solution entered the plants but was then lost into the surrounding water.

METHOD 2

Small plants 1 meter or less in length and collected near the Biological Station were brought into the laboratory and kept in running sea water in concrete trays. The effort was made to simulate

normal conditions and at the same time introduce into the plants salts for which tests could be made. One or two fronds of a plant were floated in a pan containing a 0.001% solution of lithium chloride in sea water; the rest of the plant was left in the running sea water.

On July 26 one specimen with a stipe of 46 cm and fronds of 32 cm length had the whole of the fronds up to 4 cm from the base immersed in the lithium solution. On the following day it was removed, thoroughly washed and split lengthwise; the halves were then dried over a drying box. When dry, sections were cut from the central portion of the frond 12 cm from the base and tested. These all showed strong tests for the presence of the salt. At a point 3 cm from the base of the fronds no more positive tests could be obtained. Sections taken from the stipe and adjoining fronds likewise showed negative tests.

A number of additional plants were examined as described above and all the results were found to coincide. In cases in which the plants were left in the solution for 36 hours or longer slight movements beyond the immersed portions were perceptible; such movements were never more than 1 or 2 cm. These could be accounted for solely on the basis of diffusion. The indication is that there is no transfer of water and mineral salts from the fronds to other parts of the plant.

The investigation was extended to determine whether or not any movement takes place from the holdfast and stipe up into the fronds. On July 29 about 25 to 30 cm of the stipe and holdfast of one plant was immersed in a 0.001% sea water solution of lithium chloride. Portions out of the water were well protected from drying by being covered with moist pieces of filter paper.

The plant was removed from the solution after 48 hours, carefully washed, then dried as tested before. No lithium was found to be present in the holdfast. All of the stipe which had been immersed showed strong positive tests; these tests, however, became markedly faint at the point where the stipe was out of the solution. The salt was found to be completely absent from the stipe above this point and likewise from the fronds. Masses of sieve-tubes, scraped from the wall of the pneumatocyst, showed no test for the presence of lithium when taken from a point more than 2 or 3 cm above the region immersed in the solution.

The results recorded above were checked by additional experiments. No upward movement of the salt was found to take place other than that which could be accounted for by diffusion through the material of the stipe. The faintness, or the lack, of positive tests in

the region of the holdfast indicated a lesser ability on the part of the cells of this region to absorb water and salts from their surrounding medium.

SUMMARY AND CONCLUSIONS

1. The gross anatomy of the plant is such as to lead one to believe that there may be a translocation of water and other materials. All parts of the plant, however, appear to be capable of manufacturing food and absorbing materials from without.

2. The introduction of lithium solutions into the stipes by means of a hypodermic syringe was rendered difficult by the mucilaginous character of the plant. Solution injected into the fronds was apparently lost into the surrounding water.

3. When the fronds were immersed in very dilute solutions of lithium no movement of the salt into regions of the stipe and holdfast was obtained.

4. Stipes immersed in the same strength of solution showed negative tests a few centimeters above the solution.

5. All movements of lithium recorded were so slight that they could be accounted for on the basis of diffusion. The indication is that there is no translocation of water and mineral salts in *Nereocystis*. While no tests were made to detect any possible movements of proteins and carbohydrates, it appears that such movements would have resulted in a transfer of the lithium.

6. The above investigation was carried out between July 11 and August 10, and all conclusions must be considered as applying to that season only.

Fertilization In *Stichopus Californicus*

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The large sea cucumber, *Stichopus californicus* Clark, is found abundantly in the waters adjacent to the Puget Sound Biological Station, from the rocky shore line to a depth of 80 meters. It should be a valuable form to use in the study of invertebrate embryology, due to its large transparent eggs, and the accessibility of the animals. The difficulty in the past has been to get fertilization and cleavage following insemination. This paper is the result of work done during the summers of 1926 and 1927 in an effort to find some of the factors involved. Due acknowledgement is here given to Dr. J. E. Guberlet, under whose direction this work was carried out.

The spawning season of *Stichopus californicus* seems to be during late July and August, when the animals in the shallow shore water liberate the sex cells into the sea where fertilization takes place. It is a well known fact that these animals frequently discharge their viscera when irritated or handled. On this account it was necessary to remove the gonads at the time the animals are taken. The gonads with their escaping sex cells were placed in pint fruit jars and brought back to the Station float. The jars were sealed and kept immersed in sea water until they were put in place at the Station float. During the experiments the jars were lowered on 120 cm of cord, at the float, so as to keep the surroundings, especially the temperature, as normal as possible. To be sure that variations in temperature, etc., would not affect the experiments, an analysis of the sea water was made at Brown Island where the animals were taken, and at the Station float where the eggs were kept. The averages determined are shown in table 1.

TABLE 1. *Comparison of sea water at Brown Island and at the Station float at low tide on July 14, 1927, with the air temperature at 14.6° C.*¹

Place	Time	Temperature	Salinity	Depth, in feet	pH	Ml Na ₂ S ₂ O ₃
Brown Island Station Float	10:30 a.m.	10.1	17106	1	8.2	9.14
	11:25 a.m.	10.1	17207	5	8.2	9.40

¹This determination was made by the Department of Chemistry and Chemical Engineering of the University of Washington.

The only differences in the sea water between the two locations were in salinity and in the dissolved oxygen content measured by the $M1 Na_2S_2O_3$. The Station float has a slightly higher salinity value and very little more dissolved oxygen than Brown Island, but as the jars were filled at the latter location, these variations would probably have little bearing on the problem of fertilization.

Undoubtedly *Stichopus californicus* spawns chiefly in the shallow water along the rocky shores, a region indicated by observations made during the summers of 1926 and 1927. In making collections along the shore, an accurate count was made of the animals which were sexually mature. Sexual maturity was determined by opening the animals as soon as taken and observing the gonads. Mature animals had well filled gonads which readily lost their sex cells when broken. The animals were found and tested while dredging in the open waters of Puget Sound in the vicinity of Friday Harbor at depths varying from 16 to 80 meters. The results of the examinations are given in table 2.

TABLE 2. Observations on the sexual maturity of *Stichopus Californicus*

	Number animals examined	Number animals mature	Number animals immature	Percent animals mature	Depth in meters
July 20 to Aug. 10, 1926.....	150	112	38	74	shore
July 20, 1927.....	30	18	12	60	shore
July 28, 1927.....	25	18	7	72	shore
Aug. 3, 1927.....	24	20	4	83	shore
Aug. 4, 1926.....	50	2	48	1	16-80
Aug. 1, 1927.....	21	0	21	0	16-80

The object of the first set of experiments was to determine the effect of temperature on the fertilization and cleavage of the eggs. Fertilization was determined by the formation of a fertilization membrane and the loss of the nucleus in the egg. The method followed in this experiment was to divide the eggs of sexually mature females into two portions, placing them in fruit jars filled with fresh sea water. Half of the jars were left in the shade of the Station float, and the other half immersed in 120 cm of sea water. Thus the eggs from each animal were tested as to the effect of the temperature. Insemination of both was made at the same time with fresh sperm from a mature male. The average percentage of fertilization in six experiments is shown in table 3.

TABLE 3. *Effect of temperature on the development.*

Place	Temperature	Fertilization	Cleavage	Gastrulation
Surface of float	14.4	70	25	0
120 cm in water	10.0	85	76	65

In the earlier experiments it was quite difficult to get fertilization to take place, and there seemed to be an indication that the eggs should ripen or age outside the body before fertilization could occur. This led to some experiments to try to determine this point. It was discovered that mature eggs of various ages inseminated with fresh mature sperms apparently do not require a ripening period before fertilization can take place as shown in the following average percentages:

Age of eggs in hours.....	0	1	2	3	4	8	16	24	48
Percent of fertilization.....	69	69	68	68	67	66	50	45	10

Sperms of various ages were chosen to test their respective fertilization power, with the following average percentages:

Age of sperm in hours.....	0	1	2	4	6	10
Percent of fertilization.....	85	80	65	50	34	15

These observations indicate that insemination should take place as soon as possible after the eggs are removed from the ovaries. By using fresh mature eggs, and fresh mature sperm, with insemination occurring as soon as possible, fair results are to be expected if the temperature is kept as low as fresh sea water. The average percentage reaching fertilization, cleavage, gastrulation, and the larval stages in eggs treated in this way is given in table 4.

TABLE 4. *Percent secured for various stages of development.*

	Fertilization	Cleavage	Gastrulation	Larva
July 21, 1926.....	85	76	65	10
July 28, 1926.....	85	65	54	9
July 20, 1927.....	89	44	20	0
July 28, 1927.....	69	37	34	0
Aug. 3, 1927.....	65	30	20	0

SUMMARY

1. *Stichopus californicus* is a valuable form for use in the study of invertebrate embryology.

2. The spawning season occurs during the latter part of July and August.

3. Apparently only those animals in shallow water are sexually mature in July and August.

4. The temperature at which eggs are kept is probably one of the greatest factors in the problem of fertilization and cleavage.

5. There seems to be no necessity for the eggs to ripen after their removal from the animal.

6. There undoubtedly is some internal condition concerned with the ripening of the eggs before liberation which controls the fertilization factor.

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Observations on *Pteris Aquilina*

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Large leaves of *Pteris aquilina* measured by Charles J. Chamberlain¹, while studying Cycads in Mexico and New Zealand, were 4.5 and 6.3 m high respectively. On San Juan Island leaves ranging between 1 and 4 m high were observed within a few meters from ferns barely attaining a height of 30 cm. The extreme variation in size suggested a study to determine if this difference was due to a definite factor. Other characteristics of the plant were noted and will be mentioned in this paper.

FRONDS

Within a few minutes walk from the Puget Sound Biological Station a great number of leaves were found averaging 3 m in height, with petioles 12-15 mm in diameter. They were growing in an open space surrounded by tall *Pseudotsuga taxifolia*, which protected them from direct sunlight and prevented rapid evaporation by the wind. Near them in the soil collected upon the rocks both in the woods and in the open, ferns were found growing under semi-zerophytic conditions. The soil was very scant and the rock afforded a rapid runoff for the rain water. The leaves of these ferns were 15-45 cm in height and the petioles 3-5 mm in diameter. The presence of shade seemed to have considerable effect upon the size of the leaves, giving the extremes in height. This variation in size confirms Boodle² who has shown how the leaves of *Pteris* vary and may be classed as shade and sun leaves. Injury to the leaves caused by breaking, trampling or digging the ground seemed to result in the formation of smaller leaves the following year. It was noticed on roads used for hauling wood and where trails had been broken the previous year, that only small leaves were produced. A series of sand dunes 3-5 m high was found running northeast and southwest near the fish traps at Cattle Point. Except for a few open spaces they were literally cov-

¹This information was obtained from Dr. Chamberlain of the University of Chicago, during a conversation.

²Boodle, L. A., The structure of the leaves of the bracken (*Pteris aquilina*, L.) in relation to environment. Jour. Linn. Soc. London, 35:659, 1904.

ered with *Pteris*. Leaves 20-50 cm high were found regularly. The edge of the bluff near the light house at Cattle Point faced the prevailing winds so that its leeward side was quite protected. Small leaves 20 cm high were growing on the crest of the bluff, but within a distance of 2 m on the leeward side, leaves reached a height of 1.5 m. Moisture was found at the surface underneath them in quantities sufficient to support a growth of grass. A level field in the same locality had ferns of an equal height and smaller. The wind was plainly the greatest factor in limiting moisture in this particular example.

EXTERNAL STRUCTURE OF THE RHIZOME

The rhizomes of 229 specimens growing in the woods were examined. In every instance the gross topography and size were essentially the same. The diameter averaged 10-15 mm. Roots appeared on all sides of the rhizomes. Their occurrence on top, though not as numerous as on the bottom, made the distinction of the two surfaces by the roots alone uncertain. The rhizome was divided into two distinct regions; the main stolon served for spreading and storage while the laterals served as a leaf bearing structure (Fig. 1). The laterals presented a jointed appearance, due to an increase of the angle between the frond bud and the growing tip of the lateral and to the fact that the growing tip alternated its position in relation to the frond (Fig. 5). In many plants the jointed appearance was found only in the secondary laterals. In most cases, the laterals were found to bear but one leaf during a season. Exceptional specimens had from 2-6 growing fronds on the same lateral. Many laterals had from 25-30 dead leaf bases, which would indicate in many cases the age of the lateral. However, the occasional plant having more than one growing leaf per lateral would cause one to hesitate in making an age estimate on this basis. An entire specimen of one of these plants was not obtained, but part of a rhizome 3 m in length was removed, and it with its laterals had 26 leaf bases. Rhizomes were found growing throughout the moist surface soil to a depth of 50-70 cm. A substratum of hardpan prevented growth below this depth. A number of specimens showed two series of stolons; a lower without laterals and fronds and an upper with them (Fig. 3). This arrangement was found to be exceptional and made its appearance only where the ground had been plowed some time previously. The ferns growing upon the rocks yielded rhizomes less than 30 cm long, having 3-4 growing fronds, 3-4 dead leaves and 6-15 leaf bases (Fig. 4). An additional 8-10 cm of dead rhizomes

on the end farthest from the growing tip would indicate that many of these small ferns were as old as some of those found in the woods which had rhizomes several meters in length. It appeared that size in this case was not an indication of age. Many of the plants had more than one leaf per lateral as contrasted with the tall ferns found in the woods. One plant removed from the sand dunes measured over 3 m in length and had 10 living fronds and 114 leaf bases (Fig. 2). The diameter of its stolons was found to vary greatly, ranging from 5-28 mm within a distance of 30 cm, suggesting that the stolon acted as a storage organ. Growth of the rhizome was noticeably more rapid in the dunes than any place else on the island. Roots 30 cm long having 100-150 rootlets and growing tips 2 mm in diameter were observed.

INTERNAL STRUCTURE OF THE RHIZOME

An examination was made of cross sections of 542 rhizomes. The position of the V-shaped band of mechanical tissue was found to be definite in every case. Contrary to a drawing by Bower³ it was present in the lower part of the rhizome and had its closed side down (Fig. 6). The definiteness of this band of sclerenchyma may well be used to determine the upper from the lower side of the rhizome. Many short fibers of mechanical tissue, 1-10 mm long were found scattered within the parenchyma of the rhizome. They were entirely independent of the larger two strands of mechanical tissue. In cross sections of the largest rhizomes both bands of sclerenchyma were V-shaped and both had their closed sides down. A number of the larger rhizomes were dissected with a scalpel, forceps and needle. It was found possible to remove the network of bundles entire. All of the outer bundles were found to be united (Figs. 7, 8). The large central bundles sent out branches which united with the outer bundles (Fig. 6). About half of each band of sclerenchyma went to each branch of the rhizome. A varying number of the outer bundles and about half of the three larger bundles went into the branches. Branches from the outer bundles went into the roots.

The author wishes to thank Dr. T. C. Frye and Dr. Charles J. Chamberlain for their kind assistance.

SUMMARY

1. Atmospheric moisture is an important factor in the variation in size of *Pteris aquilina* leaves.

³Bower, F. O. Botany of the living plant. Macmillan & Co., London, 1923.

2. Soil, age, structural differences and differences in the size of the rhizome have little to do with a marked variation in the size of the leaves.

3. Injury to the leaves or rhizomes may result in the production of smaller fronds.

4. The average number of leaves per year is one per lateral, but exceptions make it impossible to tell the exact age of the plant by counting them.

5. The upper side of the rhizome may be definitely differentiated from the lower by the position of the bands of mechanical tissue.

6. *Pteris aquilina* may act efficiently as a sand binder.*

PLATE 15

Pteris aquilina

b - branches	r - roots
br - branches	s - main stolon
c - connecting bundles	sc - sclerenchyma
co - cortex	sm - small fibers of sclerenchyma
d - dead leaf bases	sv - small bundles
g - green leaves	t - growing tip of lateral
l - laterals	v - large bundles
p - parenchyma	

Fig. 1. Rhizome taken from the woods.

Fig. 2. Rhizome from a sand dune.

Fig. 3. Rhizome showing two series of stolons.

Fig. 4. Rhizome from the rocks.

Fig. 5. Stages in the development of a lateral.

Fig. 6. Cross section of a rhizome.

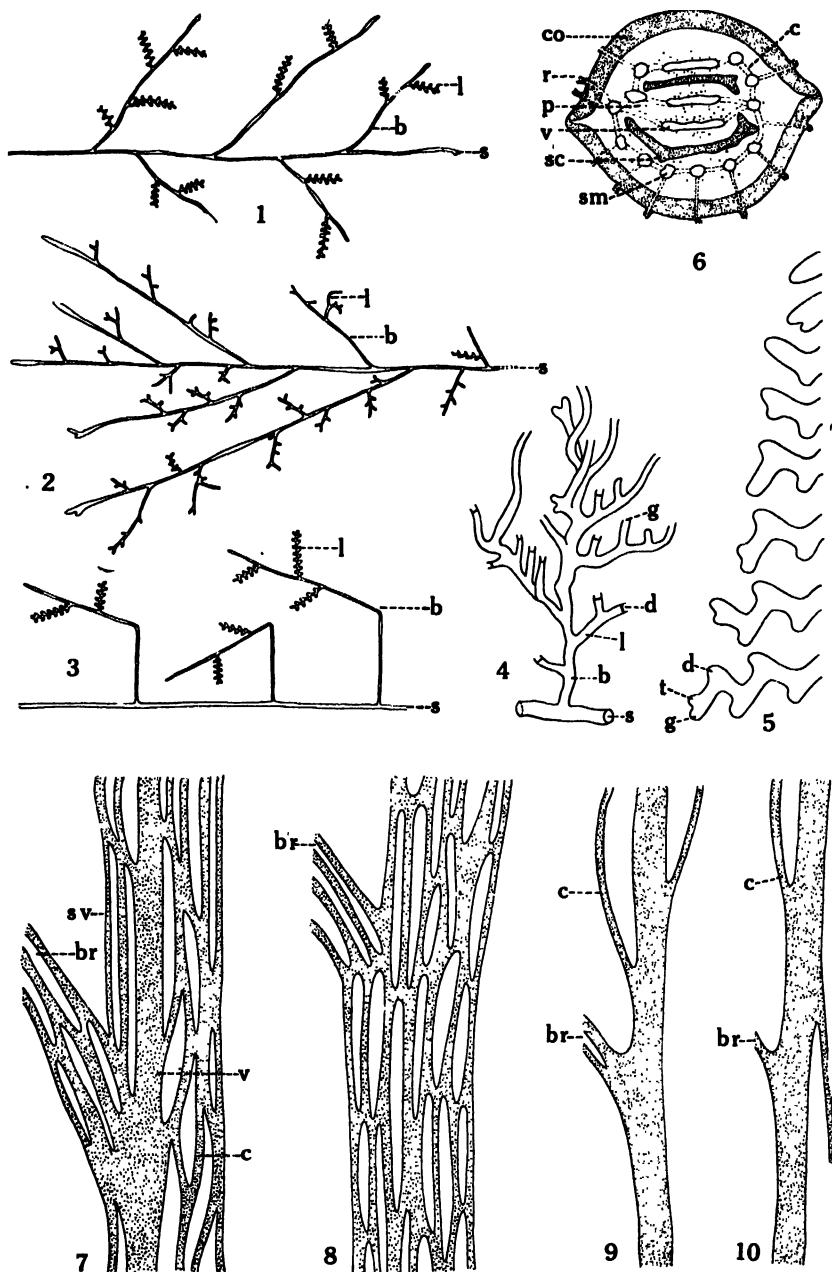
Fig. 7. Upper bundles of a rhizome.

Fig. 8. Lower bundles.

Fig. 9. Upper central bundle.

Fig. 10. Lower central bundle.

*My attention was called to this fact by Dr. G. B. Rigg.



The Holdfast of *Soranthera ulvoidea*

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This paper deals with the early development and the relation of the holdfast of *Soranthera ulvoidea* to its host, *Odonthalia floccosa*. The research was conducted at the Puget Sound Biological Station at Friday Harbor, Washington. The young and the mature plants with their host, *Odonthalia floccosa*, were gathered during a minus tide, from the rocks on the north side of Brown Island. *S. ulvoidea* may also be found at Kanaka Bay and Iceberg Point, both localities in San Juan County, Washington.

Odonthalia floccosa is a red alga that grows on the rocks of wave-washed shores. The plants grow to be about 30-40 cm in height. They are much branched, with the ultimate branchlets largely in tufts. The stem is solid in cross section, the middle portion being made up of large cells and the outer layer of small cells with many small chloroplasts. The *S. ulvoidea* is attached often to the smaller branches or in the crotch where a branch comes out from a main stem. At the time that the *S. ulvoidea* is bearing zoospores, the *O. floccosa* is producing cystocarps; hence many of the young plants of *S. ulvoidea* were found growing on old *O. floccosa* stems.

The early development of the holdfast was observed in connection with a study made of the gametophyte during the previous summer. On the union of the gametes the zygote settles down, enlarges a little, then divides (Fig. 1). This is followed by other divisions of the same kind until a plate has been formed (Figs. 2 to 10). These little plates grew rapidly in the culture dishes, both on the sides of the dishes and on slides at the bottom of the same. Their development was watched for about three weeks. In two weeks some of the cells in the plate began to divide in a horizontal plane, building upright filaments (Fig. 11). These were few at first but in a week's time a goodly number had arisen from the surface. During this time the disk was increasing in diameter and the number of free filaments becoming more numerous. Ethel Sara Barton (On the Structure and development of *Soranthera*. Jour. Proc. Linn. Soc., Botany, 33: 479-486. 1897-1898) gives a very good account of the further development; hence it will not be taken up in this paper. The

rest of the discussion will be devoted to observations on the holdfast and its relation to the host plant.

The relation of epiphytic or parasitic algae to the host has long been a problem for speculation among students of marine algae, the more so because many of these plants are wholly dependent upon one, or at least few species, for a place of attachment. *S. ulvoidea* is dependent upon two hosts. Barton, in the above paper, discusses the relationship between this plant and *Rhodomela larix*. She received dried specimens of the latter from Monterey, California. She was quite convinced that *S. ulvoidea* is parasitic upon the red alga and that she saw haustoria. The author of this paper studied fresh specimens of from less than a millimeter high to those 20 to 30 millimeters in height.

Free hand sections through the holdfast were made from plants over 3 millimeters in heights. These sections were cleared with a solution of sodium hydroxide which removed the stored carbohydrates from the cells. By this means the *S. ulvoidea* cells became greenish in color while those of the *O. floccosa* became yellowish. Four general conditions were found.

In one the holdfast completely surrounded the stem of the host, but nowhere were the cells of the host disarranged, nor even the mucilage of the outside broken. The stems of the host seemed in as healthy condition as if no holdfast were attached to them.

In another in which the holdfast did not surround the stem of the host, the latter, as before seemed in good condition with no indication that the cells of the epiphyte had penetrated or even sent in rhizoids beneath the surface layer of mucilage. No disintegration or any disarrangement of the host cells was observed.

In the third condition, the holdfast completely surrounded the stem of the host, which was broken and disintegrated on one side. Into this cavity the cells of the holdfast had crowded, but no evidence of the intermingling of the cells of the epiphyte with those of the host could be observed (Fig. 14). In every case of this kind the *S. ulvoidea* cells had filled all of the space left by the disintegration of the *O. floccosa* cells.

In the fourth, the holdfast did not encircle the stem of the host, which was broken and decaying on one side. In nearly every case of this kind the cells of the holdfast had filled the hollow but with no intermingling or evidence of rhizoids or haustoria.

Although by this method the cells of the two plants were clearly defined and good camera lucida drawings could be obtained, it was

feared that some point of interest might be overlooked. Also by this method, sections of very young plants could not be obtained.

Material was therefore gathered and classified into groups according to the size of the plants. The groups ranged from plants less than one millimeter in height to those two centimeters tall. The holdfast with a short piece of the *O. floccosa* stem to which it was attached was killed in chromacetic solution, run up by the usual histological methods and imbedded in paraffin. These pieces were sectioned with the microtome in sections 15 microns thick. The sections when mounted were stained with iron-Haematoxylin. This gave a slight contrast. However, the difference in structure was great enough to make the cells of the two plants easily distinguishable. As the sections were examined data was kept on the findings. The results were much as before with a little additional information.

The plants that were under a millimeter high separated from their host during the process of killing. This shows that the young plants were insecurely attached. At least they were not obligate-parasites, for as such, their haustoria would have penetrated the host plant almost immediately, and they would not have been so readily separated from it.

Many of the plants that were between 1 and 2 mm in height were separated wholly or in part from the host (Fig. 13). In every case where the *S. ulvoidea* was free from the host the surface of the holdfast next to the surface of the host was smooth and unbroken (Fig. 21). In no case did the surface of the host seem to have been ruptured. Of the 440 sections examined, about half showed the stem of the host to be unbroken, with no indication of penetration by the cells of the epiphyte. One-fifth of the sections revealed the holdfast separated from the host. One-third of the sections showed the *O. floccosa* stems broken and the cells of the holdfast crowded into the ruptured space. In one instance the holdfast completely surrounded the stem and filled up two breaks that were on opposite sides of the stem. The center of this stem was almost filled with cells from the holdfast; but there was no indication of haustoria or intermingling of cells between the two plants.

Of plants from 2 to 3 mm in height, 220 sections were examined. Half of them had the surface of the *O. floccosa* stems ruptured and cells of the holdfast crowded into the cavity. One case was observed in which the disintegration was on the opposite side from the holdfast. The *S. ulvoidea* cells had crept over the edge but did not fill

the cavity. If the disintegration had been caused by the holdfast its cells would have filled the entire cavity.

Two hundred and twenty sections of plants from 3 to 4 mm in height were examined. In half of these, the *O. floccosa* stems were whole, with no indication that the cells of the holdfast or haustoria had penetrated even through the mucilage of the outside. One-third of the stems were disintegrating and the cavities filled with cells from the holdfast of the *S. ulvoidea*. Here, as previously, the cells of the two plants could easily be distinguished.

Four hundred sections of plants from 6 to 8 mm in height were examined. Half of these were of whole stems. In no instance did the holdfast show any indication of penetration. In every case the surface cells of the *O. floccosa* were all intact and the stem seemed to be vigorous. The cells were well filled with protoplasm and stored food material. The number of disintegrating *O. floccosa* stems was similar to those of the previous groups examined. In one instance the cells of the holdfast were found to have penetrated longitudinally into the stem, six cells being thus found in a cavity where no opening to the surface was visible. However, in a section a few microns farther along the stem, the opening to the outside was found. It admitted a column of holdfast cells two cells in width. In no case were cells found within the *O. floccosa* stem without there being an opening to the surface. Other groups of plants were examined in the manner described, but always with the same findings.

In fixing and staining the sections, the structural differences made the cells of the two plants readily distinguishable. In the prepared sections, the protoplasts of *S. ulvoidea* with their chromatophores drew to one side or seemed suspended in the middle of the cell while those of *O. floccosa* with their numerous small chromatophores remained well distributed throughout the cell (Fig. 19). In *O. floccosa* the chromatophores lie near the periphery of the cell. These chromatophores look like small opalescent bodies when stained. Perhaps these were what Barton took to be haustoria.

SUMMARY

The holdfast of *S. ulvoidea* begins as a monostromatic disk of cells. These cells after a time give rise to upright filaments which make up the plant body and the polystromatic holdfast.

These plants grow on rocky shores which are constantly washed by heavy waves. They must have a place of security until the holdfast is large enough to withstand the wash of the water. No doubt

the mucilage and the numerous crotches of the branches of *O. floccosa* afford such security.

The fact that the holdfast plates formed readily in the glass culture dishes would lead one to believe that at least the plants are not obligate-parasites upon *O. floccosa*.

That during the time they were growing in the culture dishes they showed no sign of developing rhizoids or haustoria, and that they separated so readily from their host plants while young, would seem to prove that they cannot even be parasitic upon the *O. floccosa*.

In about half of the plants examined the *O. floccosa* stems were whole with the mucilage unbroken and the surface cells not destroyed. This would prove that the holdfasts do not injure the healthy plants, but are purely epiphytic upon them.

The fact that many *O. floccosa* stems were found in a state of disintegration with cavities extending within the tissues but with no *S. ulvoidea* plants attached; and the further fact that, when the *S. ulvoidea* plants were attached and the cavities filled with holdfast cells, there was found no intermingling of cells nor of rhizoids, would lead one to conclude that *S. ulvoidea* must be epiphytic, with the holdfast merely using available space for attachment.

Therefore the author would conclude as a result of the above findings that *S. ulvoidea* is epiphytic, not parasitic upon *O. floccosa*.

The author wishes to offer a word of appreciation to Dr. T. C. Frye, Director of the Station, for use of apparatus and the review of the manuscript.

PLATE 16

Soranthera ulvoides on *Odonthalia floccosa*

Fig. 1. First division of the zygote. $\times 365$

Figs. 2-6. Beginning of the disk of cells. $\times 365$

Figs. 7-9. Developing disks of cells. $\times 365$

Fig. 10. Disk perhaps 2 weeks old. $\times 365$

Fig. 11. Section of a disk 5 weeks old; upright filaments starting to develop. $\times 365$

Fig. 12. A disk 8 weeks old, showing many upright filaments. $\times 365$

Fig. 13. Section of a mature holdfast, showing a slight separation from the host stem. $\times 83$

Fig. 14. Section of a mature holdfast, showing a shallow rupture in the *O. floccosa* stem. $\times 83$

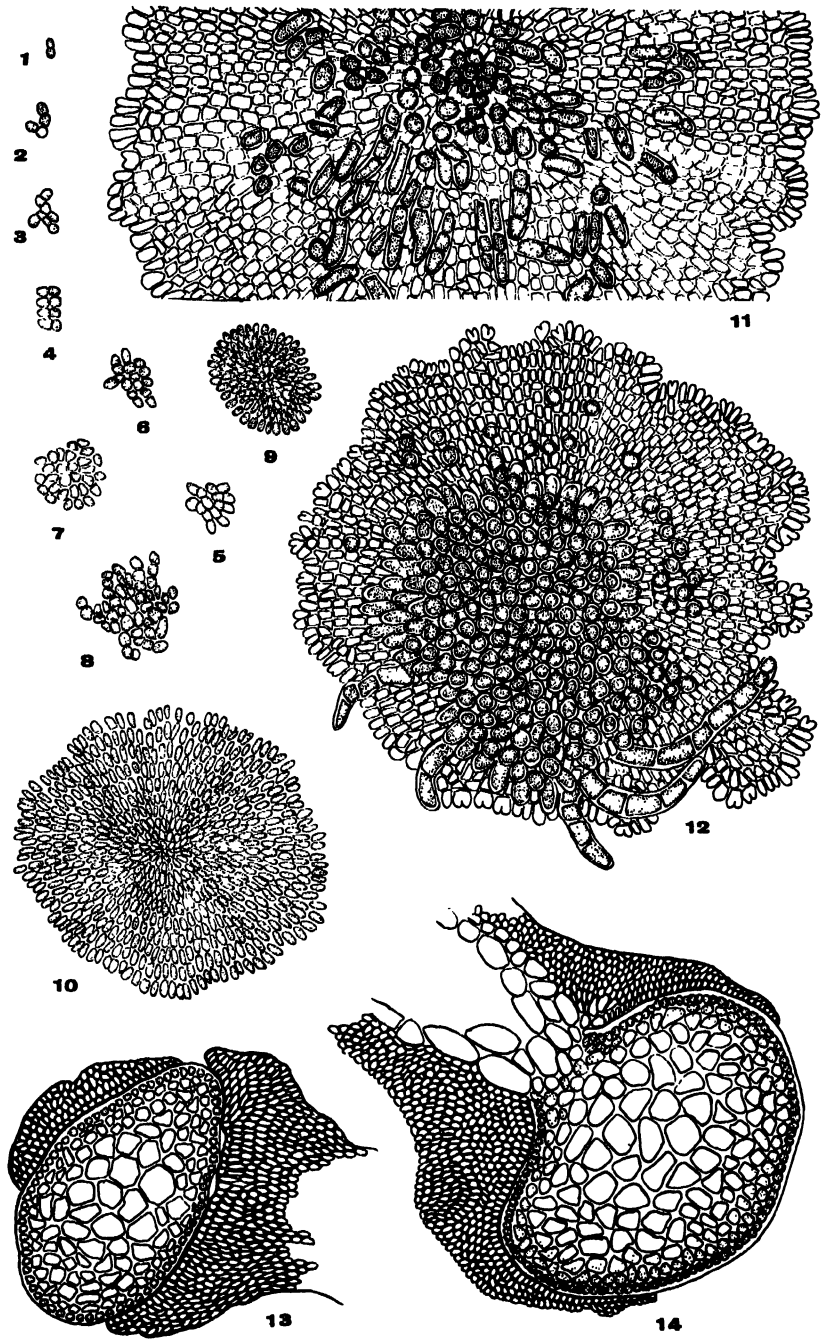


PLATE 16

PLATE 17

Soranthera ulvoidea on *Odonthalia floccosa*

Fig. 15. Section showing the character of the separation of the holdfast from the host. The cells on the left, with the small chloroplasts, are those of *Odonthalia floccosa*. $\times 209$

Fig. 16. Stem with the disintegration on the side away from the holdfast. $\times 56$

Fig. 17. The holdfast of Fig. 16 showing the cells of the holdfast (above) closely appressed to the host (below) but not penetrating it. $\times 209$

Fig. 18. Showing a break in the *O. floccosa* stem but no intermingling of the cells. $\times 56$

Fig. 19. Showing the cells of the two plants in contact, *Soranthera* above, *Odonthalia* below, $\times 209$

Fig. 20. A holdfast filling a crotch between the stem and a branch. The hollow in the *Soranthera* is visible. $\times 56$

Fig. 21. A holdfast separated from the host, showing the character of the surface adjoining the host. $\times 209$

Fig. 22. A *Soranthera ulvoidea* plant (upper) less than a millimeter high. The plant is solid at this size. $\times 209$

Figs. 23-24. Outline to show how the holdfast rests upon the host plant.

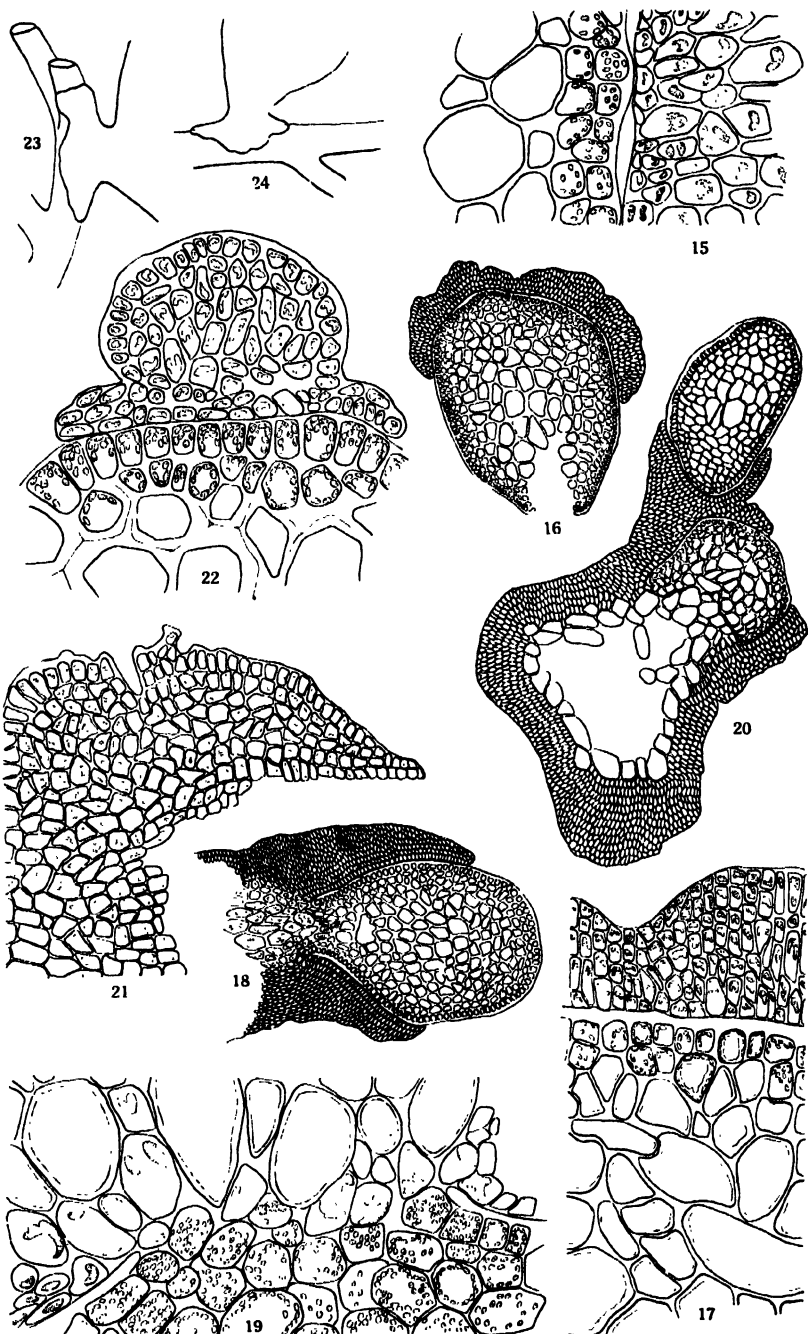


PLATE 17

The Sulfate-Chloride Ratio of the Waters of the North Pacific¹

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During the past half century a number of papers² have appeared giving the analyses of sea water from various regions of the world. In several of these papers special attention has been given to the sulfate-chloride ratio, while the data given in the others enables one to calculate this ratio.

The present investigation was begun in order to supply data concerning a region of the sea that has received very little attention from a chemical standpoint.

EXPERIMENTAL

Regions from which Samples were Collected

1. The North Pacific off the Alaskan Coast. The samples were collected by members of the International Fish Commission. Most of the samples were taken at different depths off Ocean Cape Light which is situated at the entrance to Yakutat Bay. The first series was obtained at a point 4 miles out from the Cape. Series were then gathered at intervals of every ten miles until a distance of 64 miles out from the cape was reached. A few of the samples were gathered in several estuaries or channels of the Alaskan coast.

2. The San Juan Archipelago. This group of islands lies at the northeastern extremity of the Strait of Juan de Fuca, south of the Strait of Georgia and north of Puget Sound and slightly over

¹Read before the Division of Water, Sewage and Sanitation at the 74th Meeting of the American Chemical Society in Detroit, Michigan.

²Allemandet, Bull. Inst. Ocean. Monaco, No. 88.

Clarke and Steiger, J. Wash. Acad. Sci., 1, 4.

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Hamberg, J. pr. Chem. (2) 33, 140-150.

Kolotoff, J. Russ. Phy. Chem. Soc. 24, 77-89.

Makin, Chem. News, 77, 155-56, 171-172 (1898).

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Natterer, Monatsch. 13, 873-96, 897-915 (1892); 14, 624-73 (1893); 15, 530-95 (1894); 16, 405-581 (1895); 20, 1-263 (1899); 21, 1037-60 (1900).

Ruppin, Z. anorg. Chem. 69, 232-46 (1911).

Schmelck, Norske Exped. 1882 pt. 9.

Schmidt, Bull. Acad. St. Petersburg, 24, 23 (1878).

Schoesong, Compt. rend. 142, 320-24 (1906).

Salrou, Bull. Inst. Ocean. Monaco No. 18.

Thorpe and Morton, Liebig's Ann. 158, 122 (1871).

Thoulet, Bull. Inst. Ocean. Monaco No. 12.

Wheeler, J. Am. Chem. Soc. 32, 646-9 (1910).

1,000 miles south of Ocean Cape, Alaska. The samples were collected from various stations and depths during the summer of 1926.

3. Puget Sound. This arm of the Pacific Ocean is a continuation of the Strait of Juan de Fuca and extends about 100 miles southward into the State of Washington. It covers an area approximating 2000 square miles. The samples in this region were collected from two different areas, Seattle and Shelton. The samples from Seattle, which is about 80 miles south of the San Juan Archipelago, were taken at two points about 7 miles apart. Many of the samples were collected by Isabel Colman from the surface of Puget Sound off Fauntleroy, Seattle, while the others were secured about two miles out from the entrance to the Lake Washington ship canal.

Shelton is located about 45 miles (over twice this distance via water) southwest of Seattle and near the head waters of Puget Sound. A large pulp mill, using the sulfite process began operation at this point in the late spring of 1927. All of the samples reported in this paper were collected before any of the sulfite liquor was poured into the sea. The samples were secured over an area of some 10 miles in length. A few of them were analyzed with the aid of Ronald Benson.

4. Gray's Harbor. This bay is an arm of the Pacific Ocean situated on the western coast of the State of Washington. Many small rivers empty into this body of water and samples were collected only in this region at or near the mouths of several of these rivers. A series of samples were thus secured that were diluted by natural means.

Methods of Analysis

Most of the samples were collected with the Ekman reversing water bottle. The pipets and burets used were calibrated by the United States Bureau of Standards. All measurements and titrations were carried out at 20° C.

The total halides were determined on 25 ml. of water using the Mohr method. The strength of the silver nitrate solution was such that 1 ml. equalled 10 mg of Cl and was standardized with sodium chloride and with the normal water secured from the Hydrographic Laboratories of Copenhagen.

The sulfate ions were determined gravimetrically. 100 ml. of filtered sea water were pipetted into a large beaker, acidified with 10 ml. 12 N HCl, diluted to 400 ml., boiled and precipitated with 10 ml. 3 N barium chloride solution. After standing at least 12 hours the precipitates were filtered, washed first with dilute hydro-

chloric acid and then with water and finally carefully ignited in platinum crucibles.

By precipitating the barium sulfate in dilute solution it was found that no calcium sulfate was precipitated and the amount of adsorption of other ions was kept to a minimum. Ruppin³ and van't Kruijs,⁴ using more concentrated solutions, have shown that weighable quantities of calcium sulfate are precipitated.

In table 1 are given the analyses of the waters for the halide and sulfate ions, from which the sulfate constant for the waters of the North Pacific Ocean off the Alaskan coast was calculated. There are 41 samples represented in the table. With two exceptions, there is a steady increase in salinity with the depth. The temperatures also increase with the depth until 50 fathoms (91.4 meters) is reached. Below this depth, however, there is a steady decrease in temperature to the bottom. Fig. 1 and 2 illustrate these conditions for the stations at 54 and 64 miles out from Ocean Cape Light respectively.

The average sulfate constant for these waters was found to be 0.1396, the maximum deviation from the mean being only 0.0002.

In table 2 are given the results obtained from the analyses of 21 samples of water taken from different places in the San Juan Archipelago over a one month period. The mean sulfate constant is 0.1397, the greatest deviation being 0.0005. The concentration of most of these waters was less than those given in table 2.

Table 3 contains the data secured from samples of water collected in Puget Sound in the vicinity of Seattle. The 16 samples represented were collected over a two-year period. Most of them are surface samples. The mean sulfate constant was found to be 0.1396 with a maximum deviation of 0.0003. The salinities of these waters are less than those shown in the previous tables.

Table 4 shows the results of 12 analyses of the waters of Puget Sound taken near Shelton, and represents two sets of samples taken a month apart. In this region the waters are very shallow and are affected by land drainage, the concentrations being less than those secured near Seattle. The mean sulfate constant obtained was 0.1395. The maximum deviation from the mean was 0.0010 while the difference between extremes was 0.0019. The great number of different forms of marine organisms found in these shallow waters may have been the chief cause of the deviation.

In table 5 is given the data obtained from the analyses of 12 samples of water taken in the Gray's Harbor region at or near the

³ loc. cit.

⁴ Chem. Weekblad 6, 735-58 (1909).

mouths of 4 rivers. The samples were secured at high and low tides at uniform distances from the surface and from the bed of the rivers. The sulfate constant shows a very decided variation with a difference between extremes of 0.0121. The lowest halide content of a water was 0.55 grams Cl per liter. If this result were disregarded, the difference between extremes would then be 0.0046. The mean sulfate constant for 11 of these waters is 0.1383 which is lower than that reported in all of the tables given above.

A sample of normal sea water from the Hydrographic Laboratories, Copenhagen, was analyzed and a sulfate constant of 0.1392 was obtained.

Table 6 gives the mean sulfate constant for the waters from the different regions studied.

DISCUSSION OF RESULTS

From the data presented it will be seen that the sulfate constant varies very little for ocean water of the Pacific. The variations that are noticeable occur when the waters become less concentrated. The sulfate constant obtained by us agrees remarkably well with that secured nearly 50 years ago by Dittmar for the waters of the Pacific. Dittmar analyzed 35 samples of water from all parts of the Pacific and the mean value of his recalculated⁵ results is 0.1394 with a minimum of 0.1382 and a maximum of 0.1406.

In table 7 are given the sulfate constants calculated from the results of a number of investigators. There are 551 analyses of sea water from all the oceans of the world represented. The mean of these constants is 0.13947. The minimum, 0.1363, is that of Allemandet for 103 samples, while the maximum of 0.1449 was obtained by Giral on 56 samples.

Referring to the data presented in table 6 one might conclude that the sulfate constant for sea water diluted by natural means is represented by a smaller number than that for the ocean water. This is just the reverse of that which might be expected when one considers that the sulfate-chloride ratio for fresh waters is many times greater than that for the water of the seas. This increase is such that instead of the chloride ions being the predominating ions, as in sea water, they are several times less than that of the sulfate ions in fresh waters. The sulfate-chloride ratio for the rivers in the

⁵ The accepted atomic weight for barium at the time that Dittmar worked was slightly higher than that used today. This higher atomic weight gave him a gravimetric factor for SO_4BaSO_4 of 0.34284 instead of 0.34299 and therefore his results as reported are a little low.

various portions of the United States has been calculated from available data⁶ and is given in table 8.

The possible variation of the sulfate constant of sea water due to dilution is really a minor factor, as seen from the following illustration. A sea water is assumed to have 17.000 grams of chlorine per liter and 2.3732 grams of sulfate. A river emptying into the sea contains 1 mg of chlorine and 13.2 mg of sulfate per liter. Dilution of 50 per cent and 100% will produce the following changes:

	Cl per liter	SO ₄ per liter	SO ₄ /Cl
No Dilution	17.000	2.3732	0.1396
50% Dilution	11.333	1.5865	0.1400
100% Dilution	8.500	1.1932	0.1404

In the analysis of waters near the mouth of the Fiume River, Manuelli⁷ obtained the following results:

Cl per kilo.	SO ₄ per kilo.	SO ₄ /Cl
16.47	2.303	0.1408
10.67	1.513	0.1424
9.958	1.410	0.1413
1.468	0.233	0.1600

Ruppin⁸ obtained sulfate constants of 0.1364 and 0.1378 for the relation between the sulfate and chloride ions in diluted sea water.

From these data and those presented in table 5 one concludes that variations in the sulfate constant must be due to factors other than dilution.

The sulfate constant may be affected by the adsorption of sulfate ions by the colloidal and suspended materials carried to the sea by the rivers. The coagulating power of an electrolyte depends largely upon the valence of the adsorbed or neutralizing ions. Thus the calcium, magnesium and sulfate ions, depending upon the positive or negative nature of the colloidal material, would have greater potency of coagulation than the sodium and chloride ions. Furthermore, there is the possibility of the displacement of some of the material comprising the colloidal or suspended mass by the ions contained in the sea water.

No definite data appear to be available showing the effect of various types of colloidal and suspended material upon the sulfate constant of sea water. Just recently Stowell⁹ has shown the marked adsorption of ions by sand. Calculations from the data show that

⁶ U. S. Geol. Surv., Water Supply Papers.

U. S. Geol. Surv., Data of Geochemistry, Bull. 770.

⁷ loc. cit.

⁸ loc. cit.

⁹ J. Marine Biol. Assn. 14, 955-86 (1927).

in one case the sulfate constant changed from 0.1369 to 0.1420 while in the other a slight decrease to 0.1365 was observed. However, a number of the analyses of the various forms of sediments and deposits in the sea show varying amounts of sulfate.

The different forms of marine organisms no doubt are an important factor in explaining the changes in the sulfate constant. In some of the samples taken in Gray's Harbor region small amounts of hydrogen sulfide were noted in the bottom samples. In the Wishkah River the presence of the gas has been known for a long time as implied in the name of the river itself, which in the Chinook jargon means "Stinking River."

The presence of hydrogen sulfide in the lower depths of the Black Sea was established and explained by Zelinsky¹⁰ and others. The effect of micro-organisms upon the sulfate constant is undoubtedly shown in the 6 analyses of Kolotoff¹¹ which gave a mean of 0.1353. However Burada's¹² data gives a constant of 0.1405 for a surface water.

One of us has also called attention to the occurrence of hydrogen sulfide in the Lake Washington Ship Canal¹³ in Seattle. Table 8 shows the analyses of several samples of water taken from the lower depths of Lake Union in Seattle and the marked effect upon the sulfate constant is seen. The sea water in Puget Sound near the entrance to the canal gave a constant of 0.1396 but that in Lake Union, after the removal of hydrogen sulfide, varied from 0.1342 to 0.1359.

Another factor that might cause a variation in the sulfate constant is shown in the work of Petterson,¹⁴ Hamberg¹⁵ and Ringer.¹⁶ These investigators have shown that ice retains more of the sulfate ions than chloride ion in its formation. Thus the waters under the ice will have a sulfate constant below normal and that of the melting ice above normal. A seasonal variation in the sulfate constant of waters from the polar regions might thus be noticed.

CONCLUSIONS

1. The sulfate-chloride ratio of the waters of the North Pacific and Puget Sound regions is very constant.
2. This ratio or sulfate constant is 0.1396. The amounts of

¹⁰ J. Russ. Phys. Chem. Soc. 25, 298-303.

¹¹ loc. cit.

¹² Chem. Zentr. II, 57, (1909).

¹³ Smith and Thompson, J. Ind. Eng. Chem. 19, 822 (1927). Eng. Expt. Sta. Univ. of Washington, Bull. 41.

¹⁴ Vega Exped. Rept. 2, 349-380 (1883).

¹⁵ Z. prakt. chem. 33, 140 (1886).

¹⁶ Chem. Weekblad, 37, 223-229.

sulfate per liter or kilo of sea water may be very closely estimated by multiplying the chloride content by this factor.

3. The ratio may vary in waters that are decidedly affected by land drainage and containing colloidal and suspended matter. The action of marine organisms upon the sulfate ion of sea water is also a cause for variation of the constant.

TABLE 1. *Analyses of the waters of the North Pacific, Alaskan Coast.*

Date	Depth, meters	Temperature, °C	Total halides, gm. Cl		Sulfates, gm. SO ₄ per liter	SO ₄ /Cl	Place
			per liter	per kilo.			
1-25-27	Surface	6.45°	17.55	17.18	2.453	0.1398	Revillagigedo Channel 2 miles west Hog Rock
1-26-27	Surface	4.40°	17.84	17.45	2.486	0.1394	Frederick Sound Farragut Bay
1-27-27	Surface	2.45°	17.31	16.95	2.419	0.1398	Gastineau Channel, 3 miles south of Juneau
1-28-27	Surface	5.50°	18.02	17.63	2.514	0.1395	Port Althrop, 1 mile south of Three Hill Island
1-28-27	Surface	5.95°	18.12	17.72	2.527	0.1395	4 miles south of Ocean Cape Light
1-28-27	27.4	6.22°	18.14	17.74	2.529	0.1394	
1-28-27	64.0	6.25°	18.15	17.75	2.531	0.1394	
1-28-27	Surface	5.70°	18.14	17.74	2.529	0.1394	14 miles south of Ocean Cape Light
1-30-27	18.2	5.35°	18.17	17.77	2.537	0.1395	
1-30-27	45.7	6.50°	18.40	17.99	2.565	0.1394	
1-30-27	91.4	6.50°	18.22	17.82	2.541	0.1395	
1-30-27	155.4	6.70°	18.73	18.30	2.617	0.1397	24 miles south of Ocean Cape Light
1-30-27	Surface	6.00°	18.24	17.84	2.550	0.1398	
1-30-27	18.2	5.50°	18.25	17.85	2.552	0.1398	
1-30-27	45.7	6.54°	18.23	17.83	2.543	0.1395	
1-30-27	91.4	6.87°	18.32	17.91	2.560	0.1397	34 miles south of Ocean Cape Light
1-30-27	109.7	4.82°	18.30	17.89	2.554	0.1396	
1-30-27	Surface	6.00°	18.13	17.73	2.533	0.1397	
1-30-27	18.2	6.32°	18.18	17.78	2.539	0.1397	
1-30-27	45.7	6.60°	18.26	17.86	2.551	0.1397	
1-30-27	91.4	6.75°	18.26	17.86	2.551	0.1397	
1-30-27	137.2	6.98°	18.39	17.98	2.568	0.1396	

TABLE 1—(Continued)

Date	Depth, meters	Temperature, °C	Total halides, gm. Cl		Sulfates, gm. SO ₄ per liter	SO ₄ /Cl	Place
			per liter	per kilo.			
1-30-27	Surface	6.09°	18.18	17.78	2.536	0.1396	44 miles south of Ocean Cape Light
1-30-27	18.2	5.85°	18.23	17.83	2.549	0.1398	
1-30-27	45.7	6.75°	18.25	17.85	2.547	0.1396	
1-30-27	91.4	7.05°	18.47	18.06	2.576	0.1395	
1-30-27	137.2	5.93°	18.81	18.38	2.629	0.1398	
1-30-27	Surface	6.00°	18.22	17.82	2.544	0.1396	54 miles south of Ocean Cape Light
1-30-27	18.2	6.68°	18.23	17.83	2.546	0.1397	
1-30-27	45.7	6.83°	18.66	18.24	2.606	0.1397	
1-30-27	91.4	7.19°	18.77	18.35	2.621	0.1396	
1-30-27	137.2	6.58°	18.98	18.54	2.646	0.1394	
1-30-27	182.9	6.10°	19.08	18.64	2.667	0.1398	
1-30-27	219.5	5.70°					
1-30-27	Surface	6.05°	18.29	17.88	2.553	0.1396	64 miles south of Ocean Cape Light
1-30-27	18.2	6.60°	18.36	17.95	2.561	0.1395	
1-30-27	45.7	6.60°	18.44	18.03	2.570	0.1394	
1-30-27	91.4	6.62°					
1-30-27	137.2	6.60°	19.07	18.63	2.666	0.1398	
1-30-27	182.0	6.05°					
1-30-27	228.6	5.55°	19.17	18.73	2.677	0.1397	
1-30-27	274.3	5.30°	19.18	18.74	2.681	0.1398	
1-30-27	365.8	4.50°	19.32	18.87	2.693	0.1394	
1-30-27	548.5	4.00°					
1-30-27		3.70°	19.46	19.00	2.719	0.1397	
1-30-27		3.42°	19.42	18.96	2.714	0.1398	
1-30-27	1097.3	3.25°					

TABLE 2. *Analyses of the waters of the San Juan Archipelago.*

Date	Depth, meters	Total halides, gm. Cl		Sulfates, gm. SO ₄ per liter	SO ₄ /Cl	Place
		per liter	per kilo.			
7-26-26	Surface	17.52	17.15	2.441	0.1393	Puget Sound Biological Station Blakeley Island Harney Channel Harney Channel Harney Channel
7-29-26	Surface	17.64	17.26	2.473	0.1402	
7-30-26	1	17.49	17.12	2.447	0.1399	
7-30-26	25	17.57	17.20	2.455	0.1397	
7-30-26	50	17.61	17.23	2.467	0.1401	One-half mile off Olga, Orcas Island One-half mile off Olga, Orcas Island Diamond Head Diamond Head
7-30-26	1	17.15	16.79	2.393	0.1395	
7-30-26	6	17.41	17.04	2.424	0.1393	
7-30-26	1	17.38	17.01	2.431	0.1399	
7-30-26	15	17.49	17.12	2.445	0.1398	Between Parker's Reef and the Sucia Islands
8-6-26	1	15.87	15.57	2.211	0.1393	
8-6-26	50	16.90	16.55	2.360	0.1396	
8-6-26	150	16.98	16.63	2.371	0.1396	Skip Jack Island, Amer. side of tide rip Skip Jack Island, Amer. side of tide rip Skip Jack Island, Can. side of tide rip Puget Sound Biological Station Argyle Lagoon Argyle Lagoon Cactus Island Spieden and Flat Top Island San Juan Channel, Yellow Island
8-6-26	Surface	15.91	15.60	2.222	0.1397	
8-6-26	100	18.03	17.63	2.525	0.1400	
8-6-26	Surface	16.12	15.81	2.251	0.1396	
8-13-26	Surface	17.26	16.90	2.410	0.1396	
8-16-26	Surface	17.36	16.99	2.421	0.1395	
8-17-26	Surface	17.39	17.02	2.432	0.1399	
8-22-26	Surface	17.40	17.03	2.429	0.1396	
8-23-26	Surface	17.20	16.84	2.403	0.1397	
8-23-26	Surface	17.43	17.06	2.434	0.1396	

TABLE 3. *Analyses of the waters of Puget Sound near Seattle.*

Date	Depth, meters	Total halides, gm. Cl		Sulfates, gm. SO ₄ per liter	SO ₄ /Cl	Place
		per liter	per kilo.			
2-14-25.....	30.5	16.36	16.03	2.282	0.1395	2 miles west of Lake Washington ship canal
3-27-26.....	Surface	15.66	15.32	2.191	0.1399	
3-27-26.....	152.4	16.93	16.58	2.361	0.1395	
4- 9-26.....	Surface	16.75	16.41	2.343	0.1399	Off Fauntleroy, Seattle
4-16-26.....	Surface	16.82	16.48	2.352	0.1398	
4-30-26.....	Surface	16.77	16.43	2.341	0.1395	
5-10-26.....	Surface	16.77	16.43	2.341	0.1395	
7-19-26.....	Surface	16.86	16.51	2.351	0.1394	
7-16-26.....	Surface	16.97	16.62	2.372	0.1398	
7-23-26.....	Surface	17.05	16.70	2.380	0.1397	
7-30-26.....	Surface	17.15	16.79	2.397	0.1398	
8- 6-26.....	Surface	17.16	16.80	2.391	0.1393	
1-22-27.....	Surface	16.63	16.29	2.323	0.1397	
1-29-27.....	Surface	16.57	16.24	2.309	0.1393	
2- 5-27.....	Surface	16.79	16.45	2.344	0.1396	
2-12-27.....	Surface	16.65	16.31	2.318	0.1393	

TABLE 4. *Analyses of the waters of Puget Sound near Shelton, Washington.*

Date	Depth, meters	Total halides, gm. Cl		Sulfates, gm. SO ₄ per liter	SO ₄ /Cl	Place
		per liter	per kilo.			
4-29-27.....	3.0	14.12	13.88	1.966	0.1393	Swindel's Cove
4-29-27.....	3.0	14.35	14.10	1.989	0.1386	Agate Pass
4-29-27.....	Surface	14.58	14.32	2.030	0.1392	Off Gosnell Creek
4-29-27.....	1.8	14.59	14.33	2.035	0.1395	Off Gosnell Creek
4-29-27.....	3.7	14.58	14.32	2.036	0.1396	Off Gosnell Creek
4-29-27.....	3.0	15.44	15.15	2.156	0.1397	Cape Horn
4-29-27.....	3.0	15.67	15.38	2.181	0.1392	Steam Boat Island
4-29-27.....	3.0	15.70	15.40	2.206	0.1405	Squackson Island
5-22-27.....	3.0	14.53	14.27	2.027	0.1395	Cape Horn
5-22-27.....	6.4	14.58	14.32	2.007	0.1396	Off Gosnell Creek
5-22-27.....	3.0	15.61	15.32	2.177	0.1395	Steam Boat Island
5-22-27.....	Surface	14.27	14.03	1.992	0.1396	Hammersley's Inlet

TABLE 5. *Analyses of waters at the mouth of rivers in the Gray's Harbor region, Washington.*

Date	Depth, meters		Tide	Total halides, gm. Cl per liter	Sulfates, gm. SO ₄ per liter	SO ₄ /Cl	Place
	From surface	From bottom					
6-16-26	11.3	1.5	High	7.171	1.001	0.1396	Wishkah River
6-16-26	1.5	11.3	High	3.242	0.4567	0.1408	
6-17-26	10.4	1.5	Low	9.462	1.313	0.1388	
6-17-26	1.5	10.4	Low	0.648	0.0889	0.1372	
6-17-26	9.8	1.5	High	12.850	1.790	0.1393	Hoquiam River
6-17-26	1.5	9.8	High	6.925	0.960	0.1386	
6-17-26	7.9	1.5	Low	4.615	0.6383	0.1383	
6-16-26	1.5	11.0	High	3.471	0.4785	0.1379	East Hoquiam River
6-16-26	13.7	1.5	Low	0.619	0.0848	0.1370	Chehalis River
6-16-26	1.5	13.7	Low	0.550	0.0708	0.1287	
6-16-26	6.7	1.5	High	3.937	0.5395	0.1370	
6-16-26	1.5	6.7	High	1.816	0.2473	0.1362	

TABLE 6. *Averages of constants for the sulfate-chloride ratio.*

Source of samples	Number of samples	SO ₄ /Cl
North Pacific off Alaskan coast.....	41	0.13961
San Juan Archipelago.....	21	0.13969
Puget Sound in vicinity of Seattle.....	16	0.13959
Puget Sound in vicinity of Shelton.....	12	0.13949
Mouths of rivers in Gray's Harbor.....	11	0.13825
Normal water from Hydrographic Laboratories, Copenhagen.		0.13916
Grand average (Those from Gray's Harbor excluded)....	90	0.13961

TABLE 7. *Sulfate constants calculated from the data of other investigators.*

Investigator	Number of samples	SO ₄ /Cl	Location
Allemandet.....	103	0.1363*	Atlantic, Mediterranean
Clarke and Steiger.....	1	0.1365	Gulf of Mexico
Wheeler.....	5	0.1370	Atlantic
Stowell.....	1	0.1369	Atlantic
Schmelck.....	51	0.1372*	North Atlantic
Dittmar.....	77	0.1392*	All oceans except Arctic
Schoesing.....	1	0.1392	Atlantic
Ruppin.....	12	0.1392	Atlantic, Mediterranean
Manuelli.....	6	0.1394	Mediterranean
Thorpe and Morton.....	1	0.1394*	Irish Sea
Natterer.....	42	0.1394*	Eastern Mediterranean
Thoulet.....	165	0.1400	Atlantic, Mediterranean
Schmidt.....	1	0.1400*	China Sea
Schmidt.....	2	0.1409*	Arctic
Schmidt.....	1	0.1409*	Indian Ocean
Schmidt.....	3	0.1429*	White Sea
Makin.....	22	0.1432	Atlantic
Schoesing.....	1	0.1433	Mediterranean
Giral.....	56	0.1449	Atlantic, Mediterranean
	551	0.13947	

*Corrections made for the variation in gravimetric factors due to changes in the atomic weights of barium and chlorine.

TABLE 8. *The sulfate-chloride ratio for river waters of the United States.*

	SO ₄ mg. per liter	Cl, mg. per liter	SO ₄ /Cl
The Atlantic slope.....	12.67	6.34	2.00
The Gulf of Mexico.....	17.74	6.88	2.58
Mississippi River basin.....	14.22	3.85	3.69
California rivers.....	23.32	6.90	3.38
Columbia River basin.....	12.67	1.36	9.32
Skagit River.....	17.71	1.95	9.08
Chehalis River.....	6.4	5.2	1.23
Alaskan rivers.....	13.18	1.37	9.62
Sea water.....	0.1396

TABLE 9. *Analyses of the waters from the bottom of Lake Union in the Lake Washington Ship Canal on November 6, 1926.*

Lake Union, Station No.	Depth, meters	Total halides, gm. Cl		Sulfates, SO ₄ per liter	SO ₄ /Cl
		per liter	per kilo.		
10	13.7	6.128	6.09	0.8325	0.1359
8	12.2	5.823	5.79	0.7851	0.1348
8	14.6	5.809	5.78	0.7798	0.1342

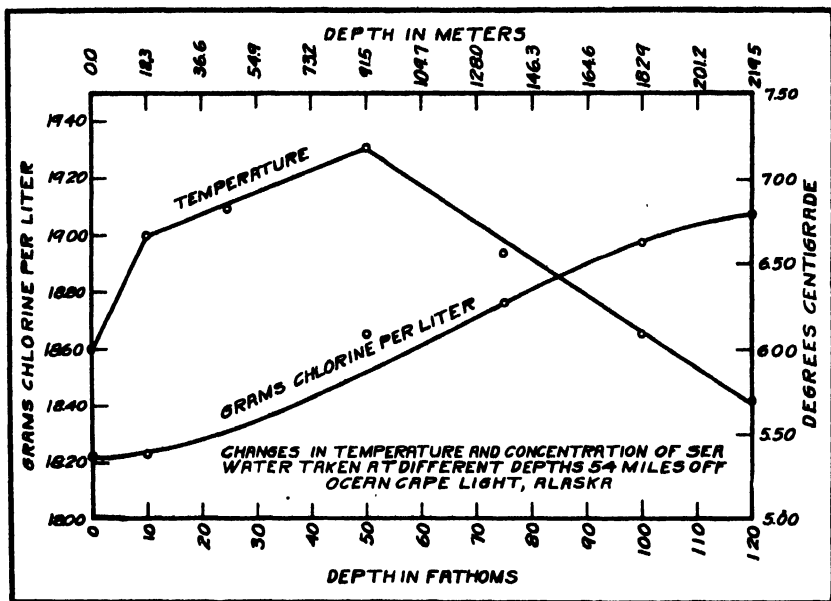


FIGURE 1

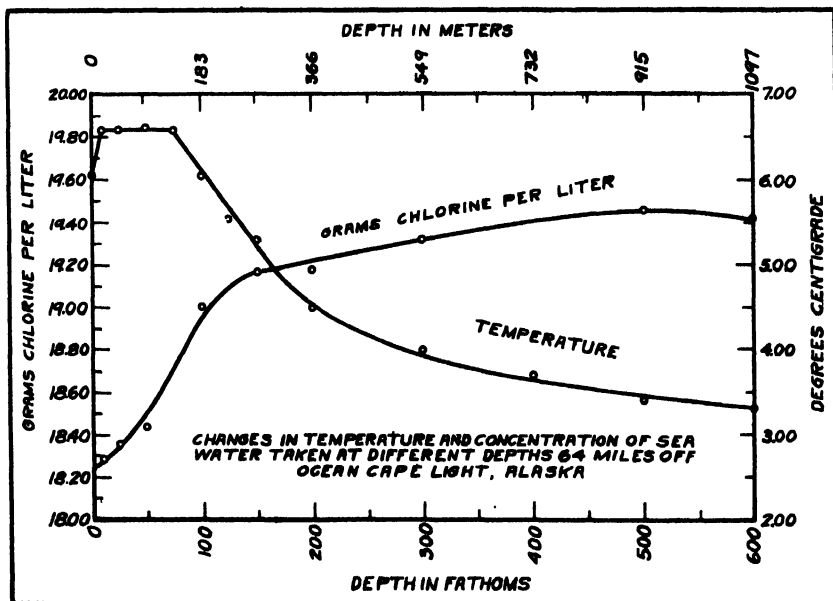


FIGURE 2

Gametophytes of *Costaria costata*

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INTRODUCTION AND METHODS

Costaria costata (Turner) Saunders is found associated with other members of the Phaeophyceae attached to the rocks, piles, or floats in the sublittoral zone. When the author arrived at the Biological Station, about the middle of June, *C. costata* plants were found already mature and fruiting, also many younger plants. This same condition was found at the middle of August when the station closed. The plants that were producing zoöspores in June were almost entirely disintegrated by the later date. The fact that fruiting *C. costata* could be found all summer facilitated the study, for zoöspores could be collected at any time during the season.

The water used in the cultivation of *C. costata* was sterilized in quart jars in a pressure sterilizer at 10 pounds pressure for 30 minutes. It was then left in the sterilizer to cool 24 hours, when it was removed and some mineral plant food added. For this purpose a small crystal each of calcium carbonate and sodium hydrogen phosphate with twice the amount of sodium nitrate was added to each quart. Glass section jars were chosen in which to grow the plants. These jars were 15 centimeters in diameter and 9 centimeters in height. They had loosely fitting covers. The jars were rinsed with sterile sea water and a quart of the culture medium was poured in. They were then ready to receive the spores.

Even in the moderate climate of western Washington it was difficult to keep the cultures from becoming too warm; hence the dishes were placed in a shallow cement tray. Water that had been cooled by passing through pipes laid under the sea for some distance was allowed to flow through the tray continually. This water remained about 2° C. warmer than that of the sea. The depth of the water in the dishes was 4.7 centimeters and that on the outside 4 centimeters.

Mature *C. costata* plants in zoöspore condition were found on a rocky shore at extreme low tide. The sori were found in irregular bands along the ribs of the fronds. From these bands pieces about 3 square centimeters in size were removed with a sharp knife. These pieces were carefully washed and placed in a bowl of fresh sea water

and carried to the laboratory. They were then washed in sterile sea water and placed in the culture dishes. In 24 hours these pieces were removed from the dishes and clean microscopic slides were placed on the bottom and against the sides of the dishes.

GAMETOPHYTES

The zoöspores of *C. costata* are large, being about 9.5×7.0 micra in size and very active. Each spore has two unequal cilia, the longer being at least 4 times the length of the spore and the shorter once the length (Fig. 18). They each contain a single peripheral chromatophore which lies toward the smaller end, leaving a clear space at the larger end. In 24 hours the spores had become quiet and were fixed upon the slides or walls of the dishes. Many of them were floating on the surface. These cultures were set up the 29th day of June. On the 2nd of July most of the spores had germinated.

For the first 20 days there was no difference observed between the male and female gametophytes. The spores sent out germ tubes, into which the contents of the spores flowed (Fig. 1). In three days the little sporelings had elongated somewhat and had begun to show some changes. Some had formed a knob at the tip into which the contents of the germ tube had passed. A transverse wall separated this knob from the germination tube (Fig. 4). Others had elongated with the protoplasm evenly distributed. By the next day many more plants had the knob at the tip. These plants seemed to rest for a day or two.

When the plants were 5 days old they resumed growth by sending out a prolongation from the knobs. It could not be determined whether all the plants took this short rest period because there always seemed to be some that did not have the knobs. In the 24 hours intervening between the 5th and 6th days the plants more than doubled in size (Fig. 5). All of them by that time had well developed chromatophores; many of them had two or three cells and all of them had at the farther end the empty germ tube and spore. These germ tubes and spores were still attached to the little gametophytes a number of days later. When the plants were 8 days old they had made considerable growth, the average width of the filaments being 5 micra and the length of many as much as 87 micra. Many plants contained from 3 to 8 cells. The chromatophores were characteristic in color, a greenish brown, and disk-shaped with no pyrenoids.

For the next 10 days the plants continued to increase in size but did not show any changes in structure except that they had begun to

branch. However, the cultures that were contaminated with diatoms or *Pelomyxa* had begun to show the effects of their ravages. Perhaps a note here concerning the destruction of the cultures by the above agents would be well.

Difficulty is always experienced in setting up cultures that are free from contamination. In spite of the careful washing and rinsing one culture was completely destroyed in 25 days by the *Pelomyxa*, an amoeba-like protozoan that would place itself in direct contact with the tiny filaments and by some means draw out the cell contents. Another culture contained diatoms which spread over the floor and sides of the dish to the destruction of the little plants. The slides from this culture were removed and washed under a stream of gently flowing water. This removed most of the diatoms. The dish was washed and rinsed in sterile water and again filled with culture medium. The slides were then replaced. These little plants were never so strong nor so far along in their development as the plants from the uncontaminated cultures. The cultures that contained a few infusoria made the best progress. No doubt these little animals consumed many of the diatoms and bacteria which would otherwise have been troublesome.

During the next few days the plants continued to grow rapidly, both in diameter and length. Some of them now measured 8 micra in diameter and were as many as 12 cells in length. It was at this time that the plants began to show a difference in structure. This was on July 28th; the plants were therefore a month old. Some of the plants were more slender than others but seemed as healthy and vigorous. At the tips of the branches of these plants were found clusters of pear-shaped cells, antheridia (Fig. 12). These were filled with chromatophores at the larger, or lower end, but the more slender tips were hyaline. With the oil immersion objective some pale chromatophores could be seen, giving evidence of cell contents. Many of the intercalary cells also formed these antheridia. Sometimes a row of 7 or 8 would be in one section of the filament.

Although the antheridia were watched every day for over a week it was not until they had become more numerous and many of them empty that some of them were observed to contain a sperm. This was an oval body with a darker spot on one side (Figs. 19, 20). No cilia were observed. In every case they were found in the hyaline tips. They measured not over 2 micra in diameter. Many of the antheridial tips were found empty and open, with yet an abundance of protoplasm and chromatophores at the base. In these cases there were more and smaller hyaline tips developing from the antheridial

cell. No doubt the antheridia go on producing sperms for some time. In a few instances two sperms were found in one hyaline tip but in every case the two were separated by a wall. These two cells were always one above the other. Although the plants were examined at various times during the day, at no time were the sperms actually seen to escape from the antheridium.

No movement was detected while the sperms were within the antheridia, and although they were clearly defined by the oil immersion objective, no means of locomotion was observed. The material was searched for free sperms but they were so nearly the size of some of the *Mastigophora* that were swimming about that one could not be sure of their identity. Some of the material was killed by placing a hanging drop containing the material over the fumes of osmic acid. Protozoans with a single flagellum and others of like size and appearance but without the flagellum were observed; but no conclusion was drawn.

The culture also contained the female gametophytes. These were larger and bore larger and longer cells at their tips. These cells were more darkly colored owing to the great number of chromatophores. By the time the culture was 32 days old many of these large end cells had been separated from the rest of the branch by a transverse wall. These were potential eggs (Fig. 23). They often measured 10 micra in diameter. Many of the intercalary cells of the female gametophyte were barrel-shaped. Often one of these cells distended to form an oogonium. Several days later some of these oogonia were observed to open and pour out their contents. The body that was extruded was at first without a definite cell wall and was not regular in shape (Fig. 27). In a short time it rounded up and became somewhat oval. The egg remained always attached to the oogonium, even after a definite wall had been formed. At no time was the exact act of fertilization observed.

SPOROPHYTE

Thirty-six days after the cultures were set up, the first sporophytes were discovered. The first segmentation in most instances divided the egg unequally. The part next to the oogonium was the smaller and was pushed back into the empty oogonium (Fig. 24). The young sporophyte was now anchored firmly to the mother plant. The young sporophyte then elongated and developed transverse walls in succession until from 4 to 7 cells had been formed in a row (Fig. 29); then longitudinal walls were developed through all the cells except one at each end (Fig. 29). The two pairs of cells above

the basal cell then usually remained quiescent, but those above put in vertical walls, thus increasing the width of the plant (Fig. 31). The cells were filled with small lens-shaped chromatophores. This monostromatic blade had its growing region at the tip, contrary to that of the mature frond, which has its meristem at the base of the blade.

The basal or rhizoidal cell began to develop after the young plant was four cells in width. The chromatophores that were carried over to it did not multiply but soon became pale in color. This rhizoidal cell elongated, pushing down the empty oogonium. When it had reached almost to the base it cut off several transverse walls. The sporophytes were at this time 15 days old. The writer could not at the time carry the observations further; however, up to this time the development of the sporophytes had been in accord with those described by C. Sauvageau (1918); probably the later development follows along the same general line.

SUMMARY

The male and female gametophytes were much alike for the first month; then a difference in size and character was observed.

The male plants were more slender and less branched. The antheridia were borne in clusters or in rows. The more or less hyaline tips bore a single sperm, which at no time was actually observed to escape.

The female plants were larger, more branched and produced a single oogonium at the tip of each branch. The egg was extruded and apparently fertilized very soon after, although actual fertilization was not observed. After fertilization the egg formed a wall and began the development of the sporophyte.

The development of the sporophytes was observed until the plants were 15 days old. By that time many of them were monostromatic plants, 4 cells in width and about 12 cells in length. No rhizoids had at this time developed but the basal cell had begun to elongate and in a few cases it had cut off several transverse walls.

The author wishes to express her gratitude to Dr. C. J. Chamberlain of the University of Chicago for suggestions concerning the preservation of material and selection of the drawings; to Mrs. Lena A. Hartge who was conducting a similar investigation on *Nereocystis leutkeana*; and to Dr. T. C. Frye, Director of the Station, for the use of apparatus and for interest shown.

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PLATE 18

Magnification $\times 418$

Fig. 1. Germinating spores 48 hours old.

Fig. 2. Germinating spores 3 days old.

Fig. 3. Four day old gametophytes showing the tips of the plants beginning to enlarge.

Fig. 4. Five day old gametophytes showing the resting stage. One plant is starting to elongate.

Fig. 5. Six day old gametophytes showing the enormous increase in size.

Figs. 6-7-8-9. Eight, nine, eleven and thirteen day old plants showing development.

Fig. 10-11. Gametophytes eighteen days old. They have begun to branch and have increased much in size.

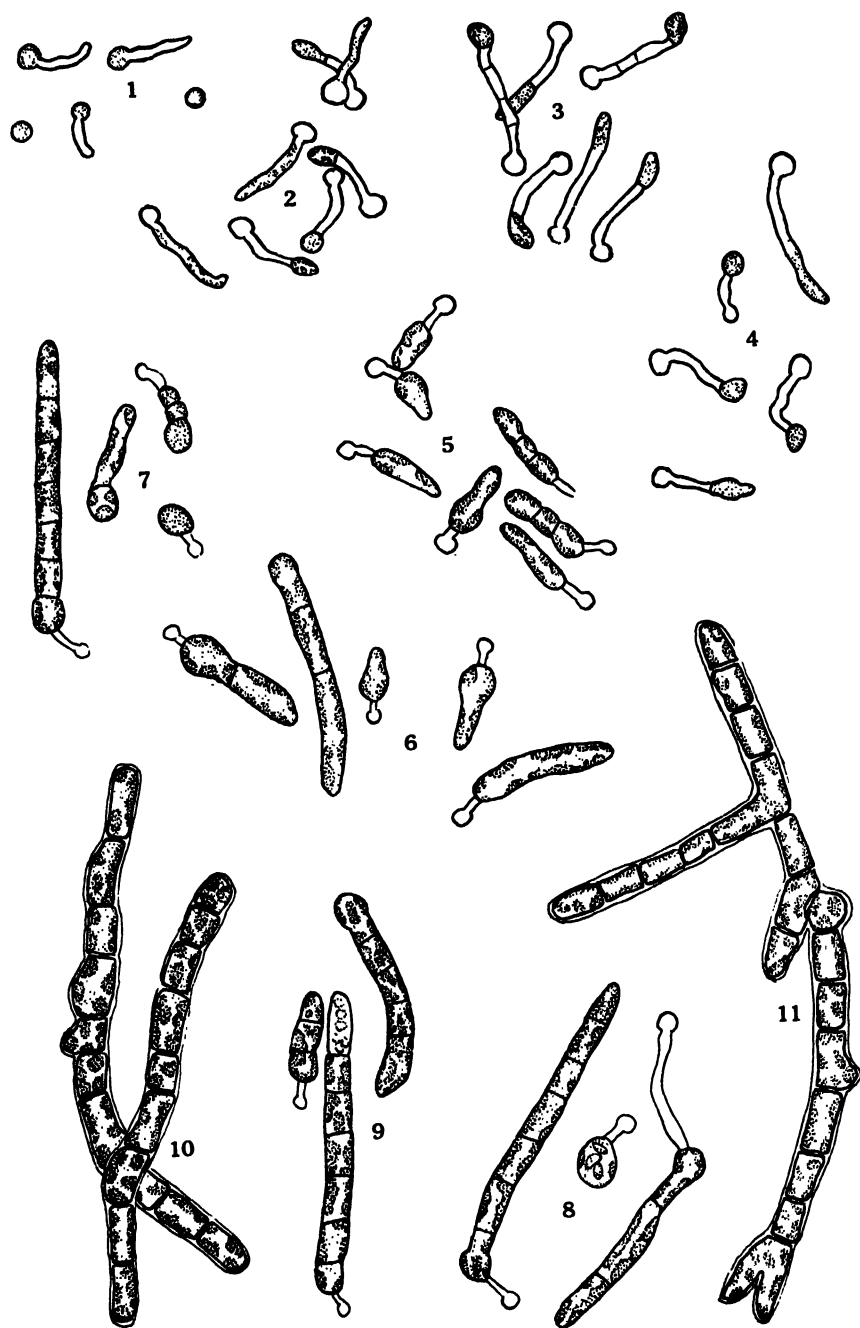


PLATE 18

PLATE 19

All of the gametophytes represented on this plate are between 25 and 30 days old.

Figs. 12-13-14. Male and female gametophytes, of the same age, showing the difference in size and appearance. The tip cells of the female plants are larger and densely packed with protoplasm. The antheridia show hyaline tips. $\times 470$

Fig. 15. Tops of female plants. One shows a young sporophyte just before cutting off the first cell wall. It is attached to the empty oogonium. $\times 470$

Fig. 16. A branch with a potential egg. $\times 470$

Fig. 17. End cell developing an egg. $\times 470$

Fig. 18. Zoospores. $\times 1150$

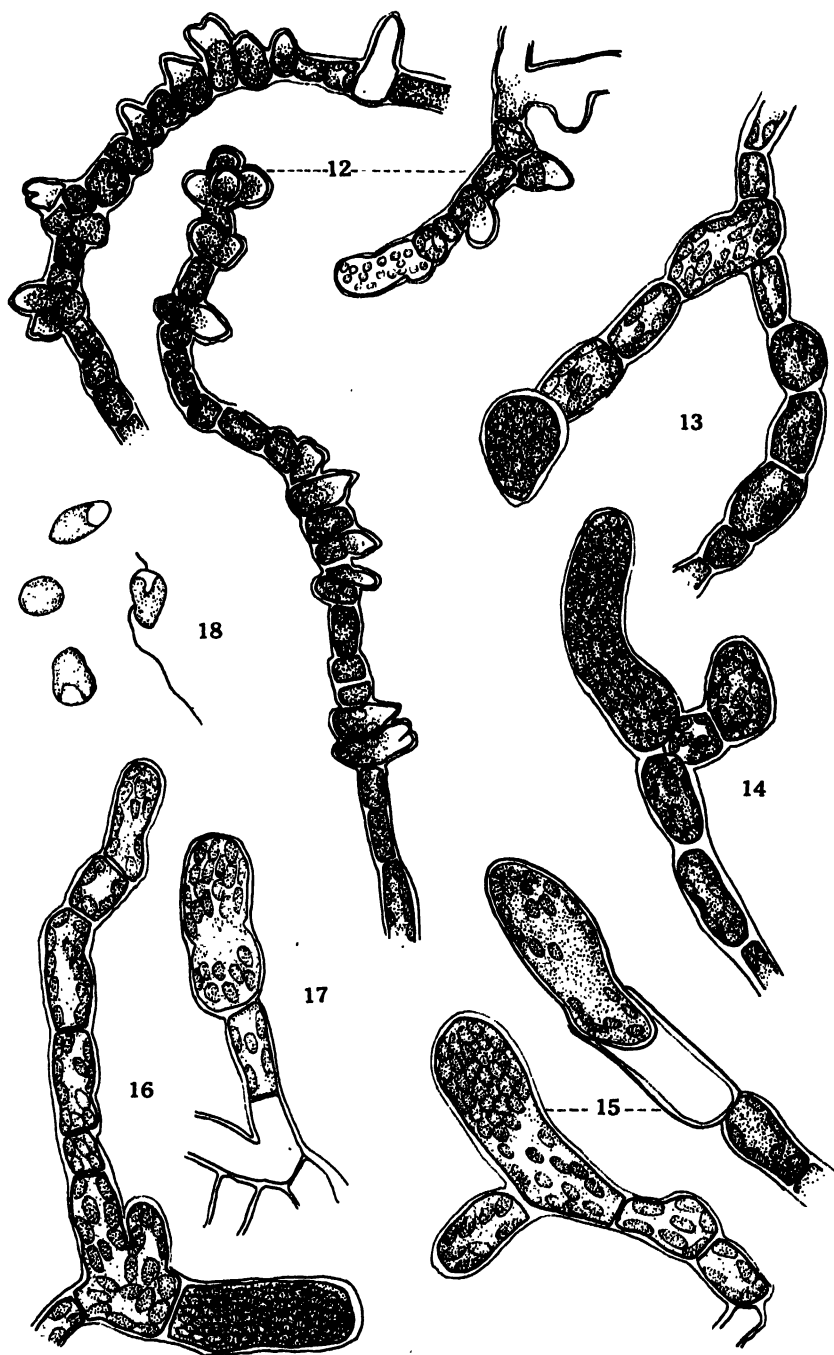


PLATE 19

PLATE 20

Fig. 19-20. Antheridial branches showing empty antheridia and antheridia containing sperms. $\times 1150$

Fig. 21-22. Antheridial branches with young antheridia in lateral and terminal groups. $\times 1150$

Fig. 23. Oögonia with potential eggs. $\times 470$

Fig. 24-25. Young sporophytes in the one and three celled stages. $\times 470$

Fig. 26. A cell of a mature gametophyte magnified. $\times 1150$

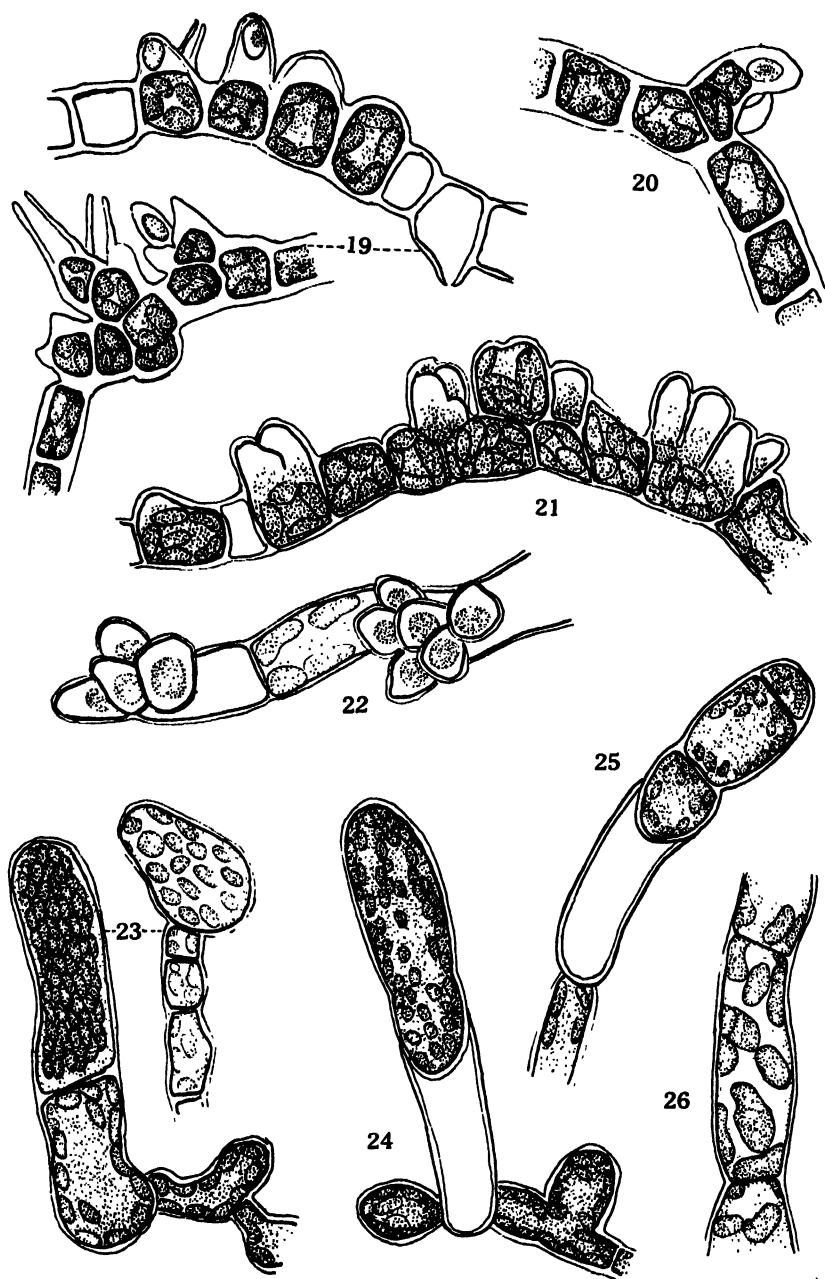


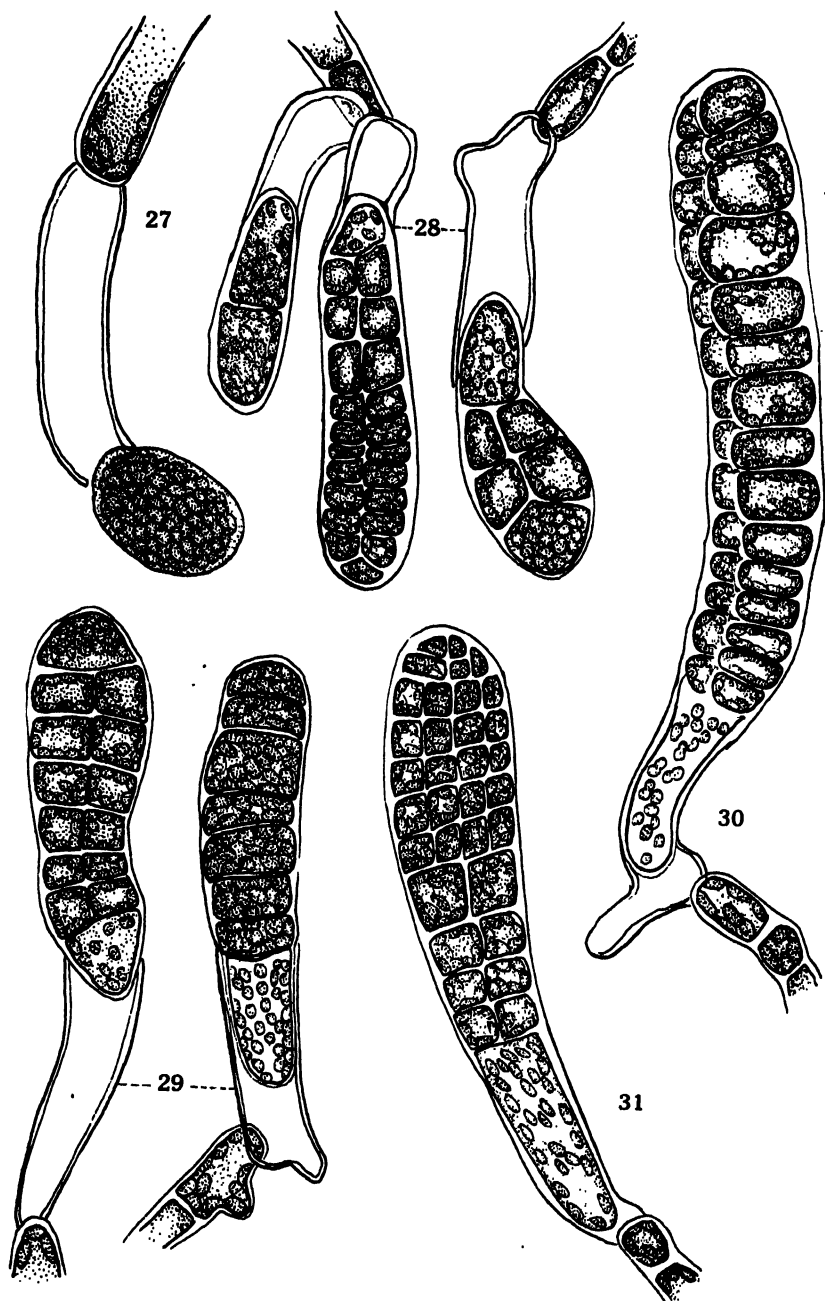
PLATE 21

Magnification $\times 470$

Fig. 27. The egg as it was ejected from the oögonium. At this time it has no cell wall.

Fig. 28-29-30. Young sporophytes in their early stages of development.

Fig. 31. Young sporophyte almost three weeks old. The basal cell has begun to elongate into the empty oögonium.



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Bibliography of Marine Bacteria

RUBY M. BOHART

University of Washington, Seattle

Oceanic waters have attracted a universally distributed corps of scientific workers. However there exists, as yet, no classification of marine bacteria, nor has any one succeeded in correlating marine bacteria with the fresh water forms. A bibliography of the marine bacteria was compiled in connection with a research problem which was completed during the spring of 1924 in the bacteriological laboratory of the University of Washington in cooperation with the U. S. Naval Station. This work has not been published, but it was deemed advisable to publish the bibliography of marine bacteria, incomplete as it may be, in order to make it available for reference for future research workers.

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Microtechnique for Marine Algae

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Morphological and cytological researches upon the marine algae present greater difficulties in microtechnique than researches upon fresh water forms, for most of the fresh water algae yield good preparations for cytological study if one merely follows available instructions for fixing, staining and mounting *Spirogyra*, *Ulothrix* and *Voucheria*; while these methods fail with many of the *Rhodophyceae*, with some of the marine *Chlorophyceae* and even with a few of the *Phaeophyceae*. A few suggestions may save time for investigators in this field and thus make more effective the limited time which most of them can spend at the seaside.

FIXING

In the *Rhodophyceae*, various forms present the greatest variety of reactions toward fixing agents. Up to date, the fixing agent which has proved most satisfactory for most forms is chromo-acetic acid with a small percentage of osmic acid (1 g. chromic acid, 1 cc glacial acetic acid and 1 cc of 1 per cent osmic acid to 100 cc of sea water). If one is particular about having the ingredients add up to just 100 parts, he can use 97 cc of sea water.

Some of the more delicate *Rhodophyceae* fix with surprising rapidity, so that in 2 or 3 minutes the fixing is complete; but if they are left in the fixing agent for 5 or 10 minutes, the cell contents become distorted and the thallus may even break up. We recommend the above fixing agent, which can be used without osmic acid if this ingredient is not available. If the material begins to break up within half an hour, try some more, watching it to find how long it can remain in the fixing agent before plasmolysis or breaking up of the thallus commences. *Polysiphonia violacea* and *P. tenuistriata* fix well in less than 5 minutes, but may be totally ruined in 10 minutes; while the coarser *Pterosiphonia dendroides* has hardly begun to fix in that time and needs over night or even 24 hours for thorough fixing.

The very delicate *Porphyra naiadum* fixes in 1 or 2 minutes, but goes to pieces within 5 minutes; while the coarser *P. perforata* should be left in the solution over night or even for 24 hours to insure proper fixing. *Bangia fuscopurpurea*, and *Griffithsia pacifica* are also deli-

cate forms which break up if left more than a few minutes in the chromo-acetic-osmic solution. On the other hand, *Pugetia fragillissima*, *Nitophyllum mirabile* and *Gigartina papillata* should remain in the reagent over night or even 24 hours.

The Corallinaceae, with their heavy incrustation of lime, offer peculiar difficulties. It is best to put the material into a 10 per cent solution of glacial acetic acid in sea water until the effervescence ceases, probably only a few minutes, and then transfer it to the chromo-acetic-osmic solution, which may act for 24 hours.

The Phaeophyceae occasion comparatively little trouble in fixing, even delicate forms like *Ectocarpus* not being likely to break up in the chromo-acetic-osmic agent already described; but there may be some plasmolysis. Where there is any shrinking of the cell contents, the acetic acid ingredient may be increased or even doubled. If there is still some plasmolysis, the chromic acid ingredient may be reduced a little, but not to exceed one half, because it is the principal hardening ingredient in this fixing agent. This will probably meet the requirements of practically every case, even the big apical cells of *Sphacelaria* and *Stypocaulon* usually showing no plasmolysis. The thallus, oogonia and antheridia of the Cutleriaceae should remain in the first mentioned fixing agent for 24 hours, and the proportion of mitoses is likely to be greater if the osmic acid ingredient is doubled or even trebled. The function of the osmic acid is to secure instantaneous killing of the cells. When only 1 cc of osmic acid is used, there is not likely to be any appreciable blackening and, consequently, there will be no need for bleaching with hydrogen peroxide, a process which, at least, does no good to cell structures, since the bleaching is always a more or less violent process. With the osmic acid ingredient as high as it is in even the weaker Flemmings solution, bleaching is always necessary. With even 2 cc of osmic acid to 100 cc of sea water, many forms will require bleaching. If one must bleach, a 5 per cent solution of peroxide, allowed to act for 20 minutes, does less damage than a 10 per cent solution, allowed to act for half that time.

In the Laminariaceae the thallus, with its spectacular imitation vascular structures, and also the sori of sporangia in all stages, fix well with the first mentioned fixing agent. The gametophytes are also beautifully fixed in the same solution. The trouble is to secure the gametophytes. No doubt they occur on the big bulbs of *Nereocystis*, on other algae, on shells and rocks, but they may be mixed with small members of the Ectocarpaceae and it is not at all impossible that taxonomists may have assigned some to this family.

Practically the only way to get these gametophytes and be sure of their identity is to grow them in cultures. No description of these culture methods would be of much practical value unless it should be complete enough to enable one to grow the gametophytes from spores. Mrs. Lena A. Hartge has perfected culture methods for *Nereocystis leutkeana* and Miss Laura Angst has had equal success with *Costaria costata*. Any one attempting to work with these forms or with any other marine algae would do well to study carefully their papers in the *Publications, Puget Sound Biological Station*. In any morphological or cytological work, the importance of a thorough study of the living material, especially the germination of spores and early stages in development, cannot be over-emphasized.

Dictyota dichotoma fixes well in the first mentioned solution. If there should be a little plasmolysis in the big apical cell, a doubling of the acetic acid ingredient will probably avoid this trouble. *Padina pavonia* is even easier to fix than *Dictyota*.

In the *Fucaceae*, this solution fixes both thallus and conceptacles with no breaking up of structures or even any appreciable plasmolysis. Centrosomes and radiations, especially in the reduction divisions in the oogonium, fix well and stain well with Haidenhain's iron alum haematoxylin. Material fixes better when receptacles are cut into small pieces, but the living receptacles collapse, so that orientation is uncertain.

The *Chlorophyceae*, with the exception of the *Siphoneae*, are not difficult to fix; but these coenocytic forms have not proved satisfactory with any of the chromic series of fixing agents. We have had better success with a formalin, acetic acid mixture (10 cc commercial formalin and 5 cc glacial acetic acid to 100 cc of sea water). In some cases the acetic acid may need to be increased. In *Codium tomentosum* 6 or 7 cc of acetic acid is likely to be necessary. In *Hormiscia*, the formula, with the acetic acid increased to 6 cc, gives excellent results. No satisfactory results have been secured with *Halimeda*, *Udotea*, *Acetabularia* and other forms which are heavily incrustated with lime; but it would probably be well, as in the case of the *Corallinaceae*, to use a 10 per cent solution of acetic acid in sea water until the effervescence ceases, and then transfer the material to the formalin acetic solution. The chromo-acetic-osmic solution might be tried, but I have never seen any material fixed in it.

Some tests were made with Diatoms and the formalin acetic solution fixed exceptionally well. The diatoms used in most of the trials were *Isthmia* and *Triceratium*; other diatoms, associated with

these, were equally well fixed. There was no plasmolysis and staining was satisfactory. These large diatoms show the nucleus and other cell contents very well if mounted whole after a careful staining in Haidenhain's iron alum haematoxylin. The Venetian turpentine method may be used after this staining, or the material can be run up through various grades of alcohol, then through several grades of alcohol and xylol, then to pure xylol, and then it can be placed in very thin balsam which should be allowed to concentrate until it reaches the proper consistency for mounting. Safranin and violet make a pleasing combination. A few drops of safranin in two or three of the alcohols used in the gradual dehydration will be sufficient. There should be no stain in the 95 per cent alcohol or in the absolute alcohol. After dehydration, a slight tinge of crystal violet in clove oil will bring out some features which might be overlooked when safranin alone is used. From the clove oil violet, the material should be brought into pure clove oil; then into xylol, and then into thin balsam which should be allowed to concentrate slowly. When the desired consistency has been reached, the material can be mounted as if from Venetian turpentine.

It has been long known that root tips fixed near noon or midnight show a larger proportion of dividing cells than material fixed at other times, and that material fixed in the middle of the afternoon may be almost entirely lacking in nuclear figures. Some observations have been made upon fresh water algae. The Cyanophyceae seem to be dividing most of the time. In the Chlorophyceae, *Spirogyra* has been examined very thoroughly and it has been found to divide most abundantly in the middle of the night, from 10 o'clock until 2 o'clock in the morning, with most of the mitoses occurring before midnight. Scarcely any divisions are found in material fixed in the daytime. Other algae which have been examined less thoroughly, but which seem to have the same periodicity, are *Zygnema*, *Ulothrix*, *Closterium*, *Cosmarium* and *Cladophora*. The infrequency of nuclear figures in fresh water Chlorophyceae fixed in the day time is a matter of common observation. Temperature seems to be the determining factor; for *Spirogyra*, brought into the laboratory and kept at a temperature below that at which mitosis takes place, will begin to divide the next morning when removed from the cooler and allowed to reach the favorable night temperature.

As far as we are aware, little has been done to determine the actual time of division in marine algae, except that investigators have noted the infrequency of figures in material collected in the day time and, in diatoms, it has been noted that figures are abundant in

material fixed in the night. The fact that in so many marine forms the spores are discharged in the morning indicates that mitosis has occurred in the night. Material of *Cutleria*, *Zanardinia*, *Dictyota*, *Fucus* and *Polysiphonia*, collected in the daytime, show enough figures for successful studies of mitoses. Whether the proportion of figures would be greater in material collected at night, has not been determined. Tides affect the fruiting periods of some algae, but whether they affect mitosis is not known.

WASHING

No material should be left in the chromo-acetic-osmic reagent more than a day or two and, as already indicated, some forms must be taken out in a few minutes; but material may be left in the formalin-acetic mixture for years without depreciating very much. After either of the fixing agents, before any staining or starting for paraffin, the material must be washed. Of course, it is washed first in sea water. Delicate forms wash quickly, coarser forms more slowly. Even the finest filamentous forms should be washed for 5 or 6 hours, and coarser forms, like sori of *Laminariaceae* and receptacles of *Fucus*, should be washed over night or for 24 hours, using running water whenever possible, and changing often when running water is not available. After washing in sea water, wash for an hour in equal parts sea water and fresh water, and then for half an hour in fresh. The material will then be ready for staining or for running up to paraffin.

EMBEDDING

Some forms can be sectioned without either fixing or embedding. The living stipes and bulbs of the big kelps cut particularly well. The sections can be studied alive and then can be fixed and stained.

For detailed work, however, thinner sections are necessary. We have found the usual paraffin method the most satisfactory. *Porphyra*, *Ulva* and *Polysiphonia* may infiltrate perfectly in half an hour, or even less. The paraffin should be changed 3 or 4 times to get rid of the xylol. Paraffin melting at 53 degrees C. should yield good sections at 3, 4 or 5 microns. If sections 2 microns thick are needed, paraffin melting at 54 degrees C. will probably be necessary. It is better to cool a 52 or 53 degree C. paraffin with ice than to use a 58 or 60 degree C. paraffin without ice, since the heat is likely to cause shrinkage. Sori of *Laminariaceae* may require about an hour in the bath. Receptacles of *Fucus* require about 2 hours. The time, in all cases, should be as short as possible.

STAINING

The most generally useful stain is Haidenhain's iron alum haematoxylin. The method is familiar to all who know anything of microtechnique; however, it may not be so generally known that after the haematoxylin has been properly drawn and the subsequent washing in water has been completed, a short stain in safranin, 15 seconds to 1 or 2 minutes, may give a beautiful rosy tinge to mucilaginous structures which would be unnoticed without the safranin.

The Flemming's triple stain, safranin-violet-orange, complete or without the orange, sometimes gives good results, but the periods are likely to be very short, in some cases not more than 5 minutes for all three stains.

Sections of the stipe of *Pterygophora* stain in safranin in 10 or 15 seconds. Light green is an effective counterstain and stains thoroughly in 1 or 2 seconds.

Paraffin sections of *Fucus*, 3 to 5 microns thick, require about 12 to 24 hours in the haematoxylin when the Haidenhain's stain is used. Safranin stains much more rapidly, but is not so good for mitoses.

Other stains and fixing agents should be tried and perhaps something more distinctly useful for marine algae would be developed.

Some of the experiments upon which these observations are based were done at Woods Hole, Mass.; some at Miami, Florida; and some at Havana, Cuba; but the most extensive experiments were made at the Puget Sound Biological Station, Friday Harbor, Washington.

For the most critical tests of the Puget Sound forms, I am deeply indebted to Miss Elizabeth Knox, Miss Marcia Fouts, and Miss Helen Hart.

The Chemistry of the Waters of Argyle Lagoon. II

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In a recent paper some of the data collected in a chemical study of the waters of Argyle Lagoon were reported,¹ together with a description of this peculiar and interesting body of water. At the time this work was done (1926) facilities were not available for the collections of samples from the bodies of water affecting the lagoon. During the summer of 1927, Dr. T. C. Frye, Director of the Puget Sound Biological Station, placed at the disposal of the authors the necessary facilities which enabled them to make a partial study of the waters immediately adjacent to the lagoon and of the lagoon itself.

Illustrations showing the directions of the prevailing currents which affect the waters of Argyle Lagoon, have been published by McLellan,² together with a description of the formation of the sand spits.

METHODS OF ANALYSIS

The methods for the analysis of chlorine and dissolved oxygen have been previously described. The pH of the samples, uncorrected for salt error, were determined by means of the LaMotte Hydrogen Ion Comparators using cresol red and thymol blue as indicators. The method used for the determination of free and combined carbon

TABLE 1. *Approximate distances between the different stations at which samples were collected*

Station No.	Location	Distances between waters in meters	Distances from Argyle Lagoon in meters
A	Griffen Bay.....	0	4000
B	Off Dinner Island.....	2300	1700
C	North Bay.....	800	800
D	Argyle Bay.....	600	300
E	Argyle Lagoon.....	300	0

¹Blalock and Thompson, Publ. Puget Sound Biol. Sta. 5:341-353. 1928.

²Geology of the San Juan Islands. Univ. Wash. Publ. Geol. 2: 139-141. 1927.

TABLE 2. *Nature and condition of samples of Argyle Lagoon and adjacent bodies of water on August 8, 1927*

Sample No.	Station No.	Depth, meters	Condition of Tide	Time	Temperature, C	Grams Cl. per liter at 20°	Grams Cl. per kilo.
1.....	A	Surface	Flood	10:20 A.M.	12.72	15.90	15.59
2.....		56-70	Flood	10:50 A.M.	9.92	17.20	16.84
3.....		Surface	Ebb	4:30 P.M.	13.30	16.10	15.79
4.....		56-70	Ebb	5:20 P.M.	10.50	17.12	16.76
5.....	B	Surface	Flood	11:00 A.M.	14.30	15.60	15.31
6.....		20	Flood	11:20 A.M.	11.38	16.71	16.37
7.....	C	5	Flood	11:45 A.M.	12.83	15.77	15.47
8.....	D	Surface	Flood	12:45 P.M.
9.....		2	Flood	1:00 P.M.	14.18	15.60	15.31
10.....		3	Ebb	4:10 P.M.	12.60	16.25	15.93
11.....	E	Surface	Flood	1:30 P.M.	19.8	15.38	15.09
12.....		3	Flood	to	18.50	17.05	16.70
13.....		Surface	Flood	2:00 P.M.	16.15	15.51	15.22
14.....		Surface	Ebb	3:40 P.M.	19.0	15.55	15.26
15.....		2	Ebb	3:55 P.M.	18.8	17.02	16.67

Sample 9 was secured in the midst of a large patch of eel grass.

Samples 11 and 12 were taken near the middle of the lagoon when water was flowing thru the channel into the lagoon. The color of the water in this portion of the lagoon was considerably different from that entering via the channel.

Sample 13 is a sample of the clear blue water taken at the surface of the lagoon near the channel.

dioxide will be published shortly in a paper dealing with this particular subject.

DISCUSSION OF DATA

Tables 1, 2 and 3 were compiled from samples taken August 8, 1927. Table 1 gives a description of the stations and the various distances between them, and the deepest portion of Argyle Lagoon.

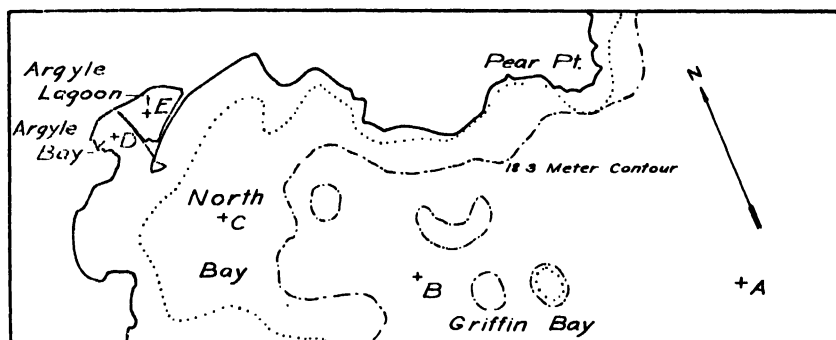


Fig. 1. Map showing the location of the various stations, designated by letters, from which samples were collected.

In table 2 are given the depths, conditions of the tide and the time at which the samples were taken, together with the temperatures and salinities (grams of chlorine per liter at 20° C, and per kilo) of the water. Table 3 gives the results of the analyses of the samples for oxygen and carbon dioxide, and the pH.

A comparison of the waters of Argyle Lagoon with adjacent waters is most easily effected by discussing each factor separately.

(a) *Temperature.* In Griffin Bay a difference in temperature of 2.80° C between the surface and bottom water existed, although the temperatures in each case are 0.58° lower at ebb tide than at the flood. Proceeding from Griffin Bay into the shallower waters of North Bay, Argyle Bay and Argyle Lagoon, a rise in temperature in both surface and bottom water is noted. The surface water of Argyle Lagoon was from 2.85° to 7.08° higher in temperature than that of Griffin Bay.

(b) *Oxygen.* With the exception of the bottom samples of Griffin Bay, the waters all contain a greater quantity of oxygen than is ordinarily found in sea water, and that of Argyle Lagoon, as previously demonstrated, is supersaturated in all cases. This is un-

TABLE 3. *Analyses of the water of Argyle Lagoon and adjacent bodies of water*

Sample No.	Oxygen		Carbon Dioxide			Mgm. CO ₂ = K Gm. Cl. per liter	pH*
	Mg. per liter	Per cent saturation†	Free CO ₂ mg. per liter	Combined CO ₂ mg. per l	Total CO ₂ mg. per liter		
1.....	8.55	93	2.49	76.31	78.80	4.80	8.3
2.....	5.89	62	5.68	85.62	91.30	4.98	8.1
3.....	8.94	99	3.20	81.81	85.01	5.08	8.4
4.....	6.27	66	2.67	77.90	80.57	4.55	8.2
5.....	10.80	121	0.31	59.03	59.34	3.78	8.5
6.....	6.73	71	8.2
7.....	9.13	100	8.3
8.....
9.....	13.08	147	0.33	55.75	56.08	8.6
10.....	8.50	106	4.52	83.13	87.65	5.12	8.3
11.....	10.35	128	0.41	67.24	67.65	4.37	8.6
12.....	14.37	181	8.7
13.....	12.10	141	0.37	60.85	61.22	3.92	8.6
14.....	11.40	140	0.53	72.87	73.40	4.09	8.6
15.....	9.75	124	8.4

*Uncorrected for salt error.

†The term "saturation" refers to a condition of equilibrium between the solution and the oxygen pressure of the atmosphere. This pressure is 168.3 mm.

doubtedly produced by the photosynthesis of the various forms of plant life which grow in greater abundance in these shallow waters. This fact has been pointed out by many investigators.

(c) *pH*. The pH of these waters increases with the temperature and oxygen content in the shallower waters, reaching a maximum value of 8.6 in Argyle Lagoon. These results are in excellent accord with those of 1926. No correction was made for the salt error.

(d) *Carbon Dioxide*. The carbon dioxide content of sea water is a variable constituent especially of coastal waters. This is due to disturbances by photosynthesis and animal metabolism of the equilibria between carbon dioxide and carbonic acid, bicarbonates, carbonates and their dissociation products.

Proceeding from Griffin Bay into Argyle Lagoon the quantity of carbon dioxide decreases markedly. The amount of free or dissolved carbon dioxide is reduced to a minimum value. That the chemically combined carbon dioxide is reduced at the same time is shown in the next to the last column of table 3 where K, the proportionality constant, has been calculated for the relation between the carbon dioxide expressed as milligrams and the chlorine as grams per liter at 20° C. It is evident from a study of the equilibria referred to above, that the same factors which produce changes in the concentration of oxygen and of the various combinations of carbonic acid on its salts are the ones which cause changes in the hydrogen ion concentration. However variations in the pH cannot be attributed wholly to these changes because of the buffer effect of other ions present in the water and effects of dilution.

(e) *Salinity* (As grams of chlorine). A very decided stratification of the waters of the lagoon is noted, a difference in depth of only 3 meters giving a difference of nearly 10 per cent in salinity. This is apparently at variance with the work of Blalock and Thompson, who found a far greater homogeneity of the water and a much higher salinity, but is easily explained by reference to tables 4, 5 and 6.

Table 4 shows the results of July 16, 1927. The samples at 1:40 P.M. were collected when water was flowing from the lagoon, while those taken at 4:30 P.M. were obtained as the water of high tide was flooding the lagoon. These samples show the homogeneity and greater salinity reported by Blalock and Thompson.

Table 5 gives the analyses of the sea water of the channel off the Puget Sound Biological Station in July and August at approxi-

TABLE 4. *Analyses of waters of Argyle Lagoon and Argyle Channel on July 16, 1927*

Time	Temp. C	Grams Cl. per liter at 20° C	Grams Cl. per kilo.	Location
1:40 P.M.....	19.5°	17.30	16.94	Lagoon (surface)
1:40 P.M.....	16.1°	17.31	16.95	Lagoon (3 meters)
1:50 P.M.....	22.0°	17.33	16.96	Channel (surface)
4:30 P.M.....	17.37	17.00	Lagoon (surface)
4:30 P.M.....	17.39	17.02	Lagoon (3 meters)
4:50 P.M.....	19.0°	17.29	16.93	Channel (surface)

mately the time at which the studies of the lagoon were made. The salinities of the two periods are markedly different, and parallel the changes in salinity of the waters of the lagoon over the same period.

The stratification of the water of the lagoon reported on August 8th is explained by referring to this table and tables 2 and 4. It is seen that the surface water of August 8th, corresponds in salinity to that of adjacent waters and to that of the Puget Sound Biological Station, but the water at 3 meters is nearer in salinity to that found on July 16th.

The bottom of portions of the lagoon is several meters below the bottom of the channel. Thus when water of a high salinity enters the lagoon it seeks the lower levels because of its density. When water of less salinity and therefore smaller density enters and leaves the lagoon, the denser water on the bottom is not disturbed. Only after periods of prolonged flushing with water of lesser density would a noticeable quantity of the heavier water be removed. As the time of low salinity is of short duration, about three weeks,³ it may be concluded that the bottom waters undergo little change in salinity. In a certain sense this is analogous to conditions encountered in Lake Union of the Lake Washington Ship Canal.⁴

Comparing the data in tables 4 and 6, of July and November respectively, and those previously reported, it will be noted that the waters of Argyle Lagoon undergo a very marked seasonal change especially in regards to temperature and dissolved oxygen. In the summer months conditions of the water in the lagoon are very different in some respects from those of sea water, while in the fall

³From unpublished data.

⁴Smith and Thompson: J. Ind. Eng. Chem. 17: 1804 (1925). Also University of Washington Eng. Expt. Sta. Bull. No. 41 (1927).

TABLE 5. *Conditions of the sea water off the Puget Sound Biological Station*

Date	Time	Tide	Surface			Depth, 12.8 meters		
			Temperature °C	Grams Cl. per liter at 20°	Grams Cl. per kilo.	Temperature °C	Grams Cl. per liter at 20°	Grams Cl. per kilo.
7-15-27	11:35 A.M.	Low	11.6	17.12	16.76	10.0	17.27	16.91
7-15-27	8:40 P.M.	High	17.36	16.99	9.8	17.43	17.06
7-17-27	7:35 P.M.	High	12.2	17.02	16.67	10.0	17.40	17.03
7-19-27	8:40 P.M.	High	10.1	17.31	16.95	10.0	17.35	16.98
8-6-27	8:00 A.M.	Low	14.1	14.94	14.67	11.3	16.74	16.40
8-6-27	7:45 P.M.	High	16.0	13.60	13.38	11.2	16.81	16.47
*8-7-27	9:00 A.M.	Low	14.0	14.52	14.27	11.6	16.40	16.07
8-7-27	7:30 P.M.	High	15.2	14.37	14.12	12.7	15.66	15.37
8-8-27	8:05 P.M.	High	14.0	15.31	15.03	12.5	15.98	15.67
8-9-27	8:05 A.M.	Low	14.1	15.08	14.81	13.1	15.60	15.31

*Dissolved oxygen of the surface water was 9.65 mg. per liter, giving a saturation of 108%, while that at 12.8 meters showed 6.91 mg. per liter with a saturation of 75%.

months the water of the lagoon is practically identical to that of the sea.

TABLE 6. *Analyses of the waters of Argyle Lagoon and the Puget Sound Biological Station on November 26, 1927*

	Lagoon	Sea water
Temperature of air.....	5.1°	8.2°
Temperature of water.....	7.3°	8.2°
Chlorine per liter at 20°.....	17.19	17.22
Chlorine per kilo.....	16.83	16.86
Oxygen, mg. per liter.....	6.22	5.92
Per cent saturation.....	62.	61.

CONCLUSIONS

1. The sea water of Argyle Lagoon during the summer months differs from average sea water at the Puget Sound Biological Station and from adjacent waters in its higher temperature, greater concentration of dissolved oxygen, greater pH and lower concentration of dissolved and chemically combined carbon dioxide.

2. During the summer months, the salinity of the surface waters of the lagoon varies with that of adjacent waters, while that at the bottom remains practically constant.

3. With the possible exception of organisms living at the bottom in the deeper portions, the differences in the marine life of the lagoon from that of adjacent waters cannot be attributed to salinity differences.

4. The seasonal variations in the waters of Argyle Lagoon are much more marked than those of adjacent waters.

Identification of Mesophilic Bacilli

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The sporulating aerobes are widespread and find their most common habitat in soil. They are carried as spores by currents of air and deposited in both fresh and salt waters where they grow readily. They form spores without the stimulating effects of drying or alteration of the temperature of the surrounding medium. The ease with which their spores are disseminated accounts for their frequent occurrence as contaminants in botanical and bacteriological cultures. The interest of early workers in bacteriology was aroused by their presence. Their presence still demands an accurate as well as rapid means of identification.

A complete description and segregation of the members of this group into species is still wanting. A number of the bacilli were described by Chester¹ in his "Manual of Determinative Bacteriology." Mace² gave a table including descriptions of bacilli in the "Traite de Bacteriologie," and tabulated a short list of special characteristics for each of the organisms. Ford, Laubach, Lawrence and Rice³ published two articles in 1916 on classification entitled, "Studies on Aerobic Spore-bearing Non-pathogenic Bacteria." They studied a total of 1700 cultures taken from soil, milk and plate contaminations. A large number of known cultures from leading laboratories of both Europe and America were used in comparison. Their work included descriptions of 28 types of which 4 were reported as new species. A committee of the Society of American Bacteriologists, headed by D. H. Bergey,⁴ completed a compilation in 1923 of the class Schizomycetes. This work included a partial description of the genus *Bacillus*.

The key presented in Bergey's "Manual of Determinative Bacteriology" involves the use of several types of media which are not readily prepared or commonly in use in a botanical or mycological laboratory. In this respect the procedure used by Bergey is hardly

¹ Chester, Frederick D., *Manual of Determinative Bacteriology*, 1901.

² Mace, E., *Traite de Bacteriologie*, 2: 585, 1913.

³ Lawrence, J.S. and Ford, W. W., *Studies on Aerobic Spore-bearing Non-pathogenic Bacteria*, Part 1. *Jour. Bact.* 1: 273-319, 1916. Laubach, C. A., Rice, J. L. and Ford, W. W., *Studies on Aerobic Spore-bearing Non-pathogenic Bacteria*, Part 2. *Jour. Bact.* 1: 493-533, 1916.

⁴ Bergey, David H., *Bergey's Manual of Determinative Bacteriology*, Williams & Wilkins Company, Baltimore. Pp. 272-310, 1923.

practical in the field of botany or mycology. This is emphasized in the use of blood serum when determining the hydrolytic action of certain members of this group. The choice of the position of spores as a distinguishing characteristic makes the separation of this group extremely difficult. For example, the position of a spore in a rod 2 microns in length may be either central, eccentric, subterminal, or terminal. Obviously the terms eccentric and subterminal are meant to cover the doubtful cases of terminal or central. The observation however is usually a dubious one on the part of the student. The same type of error will undoubtedly creep in regardless of the characteristic chosen in the formation of a key.

In order to perfect a workable key the right angle key presents certain possibilities which should not be overlooked (pages 338-339). A key of this type is self explanatory and gives the reader at a glance a description of the entire field. It is brief and, at the same time, more accurate because it includes many additional facts which may be used to check the identification. Moreover it is not necessary to follow a set procedure of identification, that is, the growth on potato or some other medium might be substituted for that of agar without a complete revision of the key. The differentiation on agar in the present instance does not express a phylogenetic division, but rather an artificial one. It does not destroy the value of the key as a means of identification because there are numerous items in addition to those of the key proper. This type of key suggests a possibility that some of this group may be strains of the same species.

Continued research on a group of plants leads a worker to choose special characteristics by which he may distinguish one plant from all others. Similarly, it has been found that a number of bacilli produce characteristic growths on the simpler media, such as agar and potato, which in themselves appear to be sufficient for identification. As an example, *Bacillus niger* may be cited, with its either smooth or wrinkled growth upon agar, but its definite soluble black pigment is a distinguishing characteristic. Special characteristics have been selected for a number of bacilli (see page 337) with the hope that they may prove helpful as a more rapid means of identification. It is improbable that such characteristics may be found for all members of this group but many more may be added to the list given. Such a list in connection with a right angle key would greatly facilitate the rapidity and ease of identification.

The methods used in describing the spore-bearing mesophilic aerobes in this paper were as outlined in the Manual of Methods and the Chart of the Society of American Bacteriologists. The time of

incubation was modified to the extent that all incubations were made for a standard time of 48 hours at a temperature of 37° C. The reason for this change was the shortening of the time necessary for identification, especially in the case of the sugars and gelatin for which more than 5 days of incubation is outlined in the chart.

All terms used in the keys presented are the same as used on the chart of the Society of American Bacteriologists. All media used in the above work were prepared under the standard conditions and formulae outlined in the Manual of Methods.

The organisms studied were obtained in part from the American Type Culture Association, and in part from the Department of Bacteriology of the University of Washington. The latter included members of the collection of Ford, and cultures isolated and identified by Dr. John Weinzirl (bacteriology).

The author wishes to thank Dr. John Weinzirl and Dr. T. C. Frye for their kind interest and assistance.

INDENTED KEY TO THE SPECIES

Numbers refer to the list at the end

A. White on agar.

B. White on potato.

C. Starch hydrolyzed.

D. Gelatin stab liquefied infundibuliform.

E. Clouding absent in bouillon.

F. Acid in lactose. 1. *Bacillus albolactus*

FF. Neutral in lactose.

12. *Bacillus megatherium*

EE. Clouding strong in bouillon.

Bacillus tumescens

DD. Gelatin stab liquefied stratiform.

10. *Bacillus mycoides*

DDD. Gelatin stab liquefied crateriform.

2. *Bacillus adherens*

CC. Starch not hydrolyzed. 13. *Bacillus prausnitzii*

BB. Buff on potato. 6. *Bacillus cereus*

BBB. Pink on potato. 16. *Bacillus subtilis*

AA. Yellow on agar.

G. Yellow on potato.

H. Nitrate reduced. 7. *Bacillus fluorescens*

HH. Nitrate not reduced.

- I. Gelatin stab liquefied infundibuliform. 14. *Bacillus petasites*
- II. Gelatin not liquefied. 9. *Bacillus lautus*
- GG. Gray on potato. 3. *Bacillus aterrimus*
- AAA. Buff on agar.
- J. Buff on potato.
- K. Starch hydrolyzed.
- L. Nitrate reduced.
- M. Surface growth on bouillon, a ring.
Bacillus flexus
- MM. Surface growth absent on bouillon.
Bacillus simplex
- LL. Nitrate not reduced. *Bacillus flavus*
- KK. Starch not hydrolyzed.
- N. Nitrate reduced.
- O. Alkaline in lactose. *Bacillus terminalis*
- OO. Neutral in lactose. 15. *Bacillus panis*
- NN. Nitrate not reduced. 4. *Bacillus badius*
- JJ. Brown on potato.
- P. Nitrate reduced.
- Q. Gelatin stab liquefied stratiform.
- R. Surface growth on bouillon a pellicle.
Bacillus coherens
- RR. Surface growth on bouillon a ring.
Bacillus fusiformis
- QQ. Gelatin stab liquefied crateriform.
Bacillus brevis
- PP. Nitrate not reduced.
- S. Gelatin stab liquefied stratiform.
Bacillus agri
- SS. Gelatin not liquefied. *Bacillus pseudotetanicus*
- BBB. No growth on potato. *Bacillus tritus*
- BBBB. Pink on potato. 17. *Bacillus vulgatus*
- AAAA. Clear on agar.
- T. Nitrate reduced. *Bacillus centrosporus*
- TT. Nitrate not reduced. *Bacillus globegii*
- AAAAA. Brown or black on agar.
- U. Yellow on potato. 8. *Bacillus graveolens*
- UU. Brown or black on potato. 11. *Bacillus niger*

DISTINGUISHING CHARACTERISTICS OF CERTAIN SPECIES

1. *Bacillus albolactus* (Loeffler) Migula. Produces a four odor in milk. White on agar and potato and acid in lactose.
2. *Bacillus adherens* Ford. Gray or white rhizoid adherent growth on agar. Diastatic action positive. Some strains produce a yellowish-brown slightly soluble pigment on agar.
3. *Bacillus aterrimus* Lehmann and Neumann. Yellow then black on agar. Gray and folded on potato.
4. *Bacillus badius*. Produces an odor similar to putrid meat on agar.
5. *Bacillus circulans* Jordan. Gelatin not hydrolyzed, no growth on potato, acid in lactose. This species was omitted from the keys because the material was not at hand.
6. *Bacillus cereus* Frankland. White mealy growth with pellucid dots on agar.
7. *Bacillus fluorescens* Ford. Yellowish-green water soluble pigment produced on agar.
8. *Bacillus graveolens* Gottheil. Chocolate brown on agar producing a water soluble pigment. Pumpkin yellow on potato.
9. *Bacillus lautus* Batchelor. Gelatin no hydrolyzed. Pale brown on potato, acid in lactose.
10. *Bacillus mycoides* Flügge. White or grayish filamentous non-adherent growth on agar. Diastatic action negative.
11. *Bacillus niger* (Gorini) Migula. Produces a black water soluble pigment on agar.
12. *Bacillus megatherium* De Bary. White viscid growth on agar with pellucid dots, becoming yellow with age.
13. *Bacillus prausnitzii* Trevisan. White or gray filamentous adherent growth on agar. Diastatic action negative.
14. *Bacillus petasites* Gottheil. Agar cultures yellow, then brown. Potato pumpkin yellow.
15. *Bacillus panis* (Vogel) Migula. Buff wrinkled growth on agar and potato. Lichen-like pellicle on bouillon.
16. *Bacillus subtilis* (Ehrenberg) Cohn. White and smooth on agar. Grayish becoming rapidly pink, either dull and dry or viscid and vesicular upon potato.
17. *Bacillus vulgatus* Flügge. Wrinkled and buff on agar. Pink moist vesicular or folded growth on potato becoming brownish with age.

RIGHT ANGLE KEY TO SPECIES OF BACILLUS					
	subtilis	cereus	prausnitzii	adherens	mycoides
Color on agar: <i>white, Black, brown, yellow, clear, or buff</i>	w	w	w	w	w
Color on potato: <i>white, brown, yellow, gray, buff, pink, or no growth</i>	p	U	w	w	w
Starch hydrolysis: <i>positive or negative</i>	p	p	n	p	p
Nitrate reduction: <i>positive or negative</i>	p	p	p	p	p
Liquefaction in gelatin stab: <i>infundibuliform, none, stratiform, crateriform</i>	s	c	i	c	s
Surface growth in nutrient broth a ring, pellicle, or absent.....	r	r	p	r	p
Clouding in bouillon: <i>moderate, slight, Strong, or none</i>	s	n	n	s	n
Lactose fermented with the formation of <i>acid, Alkali, or neither</i>	n	n	a	n	n
Dextrose fermented with the formation of <i>acid, Alkali, or neither</i>	a	a	a	a	a
Sucrose fermented with the formation of <i>acid, Alkali, or neither</i>	a	n	a	n	n
Agar colonies: Form <i>circular, irregular, rhizoid, or filamentous</i>	c	c	f	r	f
Surface <i>smooth, rough, concentrically ringed, or Radiately ridged</i>	s	s	R	r	R
Elevation <i>flat, raised, pulvinate, umbonate</i>	r	r	r	r	r
Edge of colony: <i>entire, Erode, or filamentous</i>	E	e	f	f	f
Nutrient broth: surface growth <i>flocculent, membranous, or absent</i>	f	f	m	m	f
Potato stroke: growth <i>scant, abundant, or Absent</i>	a	a	a	a	a
Form <i>filiform, echinulate, or spreading</i>	f	f	e	f	f
Lustre <i>glistening or dull</i>	d	d	d	d	d
Surface: <i>smooth, or rugose</i>	r	s	s	s	s
Agar stroke: form of growth <i>filiform, arborescent or echinulate</i>	f	f	a	a	a
Lustre <i>glistening or dull</i>	g	g	d	g	d
Surface <i>smooth, contoured, or rugose</i>	s	s	r	c	r
Odor <i>present or absent</i>	a	a	a	a	a
Consistency <i>butyrous, viscid, mealy, or Brittle</i>	b	m	B	B	b
Medium <i>unchanged, browned, yellowed, or Blackened</i>	u	u	u	u	u
Ends <i>rounded or square</i>	r	r	r	r	s
Endospores <i>central or polar</i>	c	c	c	c	c

albolactus	megatherium	aterrimus	fluorescens	lautus	petasites	flavus	flexus	simplex	panis	terminalis	badius	agri	pseudoteticus	brevis	coherens	fusiformis	tritius	vulgatus	centrosporus	globegii	graveolens	niger
w w p	w w p	y g n	y y p	y y p	y y p	U U p	U U p	U U p	U U n	U U n	U U n	U b n	U b n	U b n	U b n	U b n	U n n	U p p	c b n	c b n	b y p	B b n
p i r	p i r	p c p	p s p	n n p	n i r	n c r	p s r	p s a	p s p	p s p	n i r	n s r	n n r	p c p	p s p	p s r	p n p	p c p	p c p	n n r	p i r	p c r
n a a	n a a	n n a	m n a	n a a	n n a	n n a	n n a	m n a	n n a	n A A	S n n	m n a	n n a	S n n	n n a	n n n	n A A	n n a	m n n	n n n	n n a	n n a
a c s	a i s	n i s	n c s	a i s	n c s	n c r	n i s	n c s	n i r	A c s	n i s	n i r	n i c	n i s	n c s	n c s	A i s	a i r	n i c	n c s	n c s	a c r
u E f	r e f	r e f	r e f	r E f	r e m	r E f	f E f	r e a	p e m	r e m	r E f	r e f	r e f	f e f	r e m	r e f	r e m	u e m	r e f	f E m	r e m	r e f
a s d	a f d	a s g	a f d	a f g	a f d	s f d	a f g	a f g	a a d	a f d	a f g	s f d	s f g	a f g	a s g	a s g	A - -	a s g	s f g	s f g	a f d	a s g
s f d	s f d	r c g	s f d	s e g	s f d	r f g	s e g	s e g	r f d	s f g	s e g	s e g	s f g	s e g	s f g	s f g	- e g	r e g	s f g	s f g	s f d	s f g
s a b	s a b	s a b	s a b	s a b	s a b	s a b	s a b	s a b	r a b	s a b	s c p	c a b	s a b	s a b	s a b	s a b	s a b	r a b	s a b	s a v	s a b	s a b
u r c	u r c	u r c	y r c	u r p	b r c	u r c	u r c	u r c	u r c	u r p	u r c	u r p	u r p	u r c	u r c	u r c	u r c	u r c	u r c	u r c	b r c	B r c

A Chemical Study of the Waters of Argyle Lagoon

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LOCATION AND DESCRIPTION

Argyle Lagoon is a triangular body of water located off the eastern shore of San Juan Island, Washington, and just north of Griffin Bay. Figure 1 is a map of Argyle Lagoon showing its triangular shape and the positions of the bodies of water and the pieces of land affecting it. The lagoon is bounded on the south by a

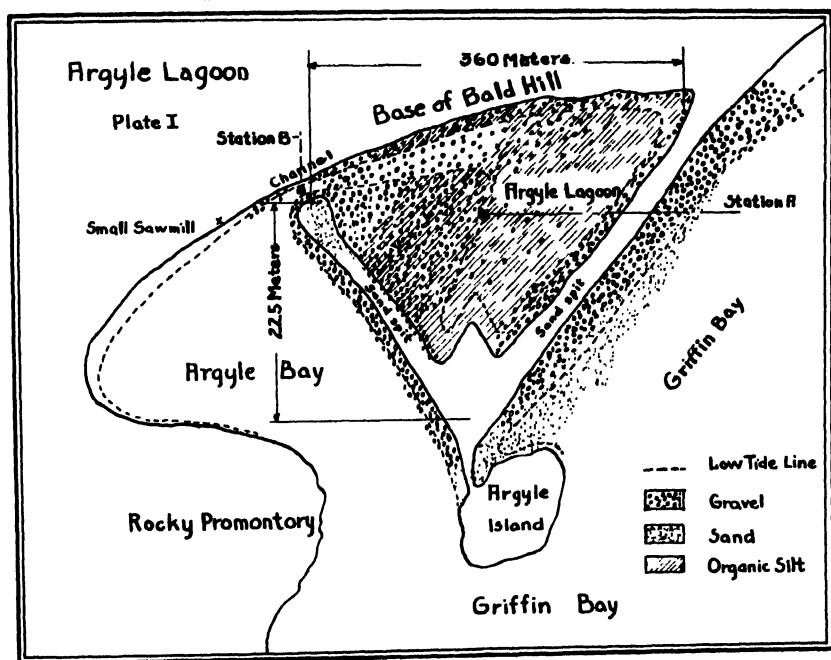


FIG. 1. Map of Argyle Lagoon.

gravelly spit which has been built up high enough so that the water in Griffin Bay does not surmount the barrier even during the severe storms of the winter months. Along the northeast side, just back of the high tide line, is the base of Bald Hill, while along the southwest boundary is a long spit of sand and gravel separating Argyle Lagoon from Argyle Bay. The northern extremity of this spit has not yet reached the land beyond the influence of the tides. The latter formation permits a channel which is the only means of exchange of water

in the lagoon during the succession of the tides. The spit at the south, separating the body of water making up the lagoon from Griffin Bay together with the spit along the southwest side, have been built up of glacial till from the hillsides. This has been accomplished by the action of waves and currents. The shape of the spit is due to the presence of the so-called Argyle Island, which may be reached by walking along the spit except during extreme high tide. Current and wave action have a tendency always to build out and connect islands and points of land by deposition of sand and gravel. Argyle Island thus serves as the apex of the triangle which encloses Argyle Lagoon and from it the two spits, formed by wave and current action, project toward the mainland.

The map also shows the nature and location of the deposits on the floor of the lagoon. The deposits are composed of sand, gravel and organic silt. That particular portion of Griffin Bay south of Argyle Lagoon is sometimes known as North Bay. Thus the lagoon is connected by a small channel to Argyle Bay, which is an estuary of North Bay and which in turn is a part of Griffin Bay.

Figure 2 is a photograph of Argyle Lagoon taken from the top of Bald Hill. Argyle Island is seen at the left with the two spits projecting to the base of Bald Hill. The channel, not shown in the illustration, is located at the extreme right and its bed is almost at right angles to that of the spit. Beyond Argyle Island and the spit, which runs nearly parallel with the bottom of the page in the illus-



FIG. 2. Photograph of Argyle Lagoon.

tration, is Argyle Bay with North Bay of Griffin Bay to the left of Argyle Island.

At high tide the body of water in the lagoon covers a triangle 360 by 225 meters and an area of about 10 acres. At the center of the lagoon during low tide, the water is three meters deep. The lagoon is unique in that there is no apparent stream or spring of fresh water emptying into it. Furthermore the water level and the outlet of the lagoon are sufficiently high so that the water flows from it through the Argyle Channel for four hours after the tide has turned in Argyle Bay. Whenever the tide is not high enough to back the water up through the channel and so empty into the lagoon, water will continue to flow from the lagoon into Argyle Bay.

Stations *A* and *B*, on the map, indicate the places where samples of water were taken for analysis. Station *A* is in that part of the lagoon where the water at low tide is three meters deep. This station was in the region of eel grass, which is covered with diatoms. At Station *A* surface and bottom samples of water were taken for analysis.

METHODS OF ANALYSIS

Dissolved oxygen. The samples were collected and analyzed according to the standard methods.¹ The bottles used for the collection of samples had capacities ranging from 230 ml to 276 ml, 100 ml being finally taken for titration. Corrections were made for the volumes of reagents added.

*Salinity.*² The salinity is given as grams of chlorine³ per liter and per kilogram of water. The Mohr method using potassium chromate as an indicator was used for the determination of chlorine. Twenty-five ml samples of water were taken for titration with silver nitrate solution, 1 ml of which was equivalent to 10 milligrams of chlorine. The grams of chlorine thus determined per liter of water at 20° C were calculated as grams per kilogram by the use of tables published by one of us.⁴

pH Determination. Phenol red was the indicator employed, using fresh standards supplied with the Hynson, Wescott and Dunning

¹ Standard Methods of Water Analysis, American Public Health Assoc. 6th ed. (1925).

² The accepted definition for salinity does not represent the dissolved material as evidenced by the definition of its determination. Its calculation from the chlorine content by the aid of the Hydrographical Tables is really nothing more than another means of expressing the chlorine content.

³ The amount of chlorine in sea water is universally defined as the grams of chlorine contained in a kilogram of water, assuming the small quantities of bromine and iodine to be replaced by chlorine.

⁴ Thompson, Thomas G. Jour. Am. Chem. Soc. (1928).

apparatus. Corrections were not made for the salt error of the indicator.

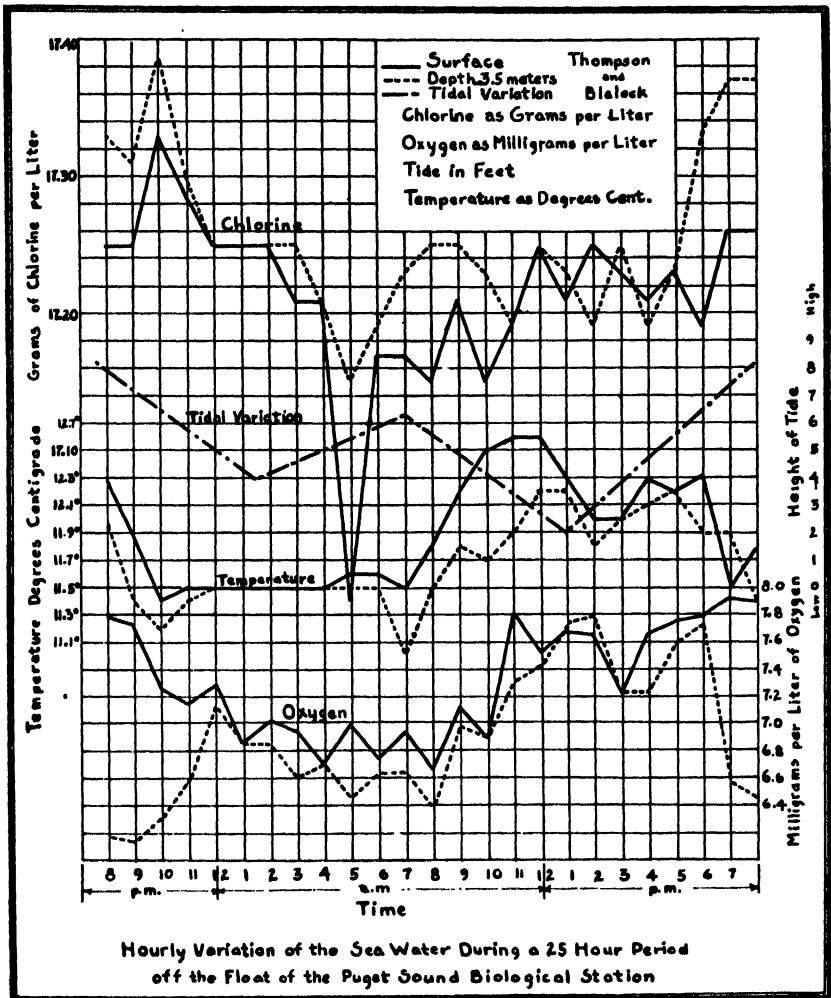


FIGURE 3

COMPARATIVE OR CONTROL DATA

In order to have a means of comparison for the waters of the lagoon a series of samples of sea water were collected from the float of the Puget Sound Biological Station. Samples were taken every hour both from the surface and a depth of 3.5 meters for a period of 25 hours.

EXPERIMENTAL

Sea Water of Puget Sound Biological Station

In table 1 are given the temperatures and the dissolved oxygen and chlorine determined on samples of sea water taken at the surface and at a depth of 3.5 meters from the float of the Biological Station. The collection of the samples began at 8:00 P.M. on August 12, 1926 and was continued hourly until the following day at 8:00 P.M. These data together with the tidal variation for the 25 hour period are shown in figure 3. From a study of table 1 and figure 3 the following facts are ascertained:

1. No extreme tides were experienced during this period. The tests started with a high tide of 8.4 feet and ended with a tide of 8.3 feet. Low tides of 4.1 feet at 1:29 A.M. and of 2.2 feet at 12:58 P.M. were noted together with a high tide of 6.4 feet between the two low tides.

2. During the period of the tests the salinity at the surface showed a maximum variation between extremes of .32 ‰ while at the depth of 3.5 meters the variation between extremes was only .23 ‰.

3. As the slack water of low tides was approached the salinity at the surface and at 3.5 meters was practically the same.

4. During the night and early morning hours there was a gradual drop in the salinity of the waters.

5. Increase in salinity was noted near the peaks of the higher tides.

6. Immediately after sunset the temperatures of the water showed a decided drop, and during the hours of darkness the temperature was constant.

7. Maximum temperatures were obtained at noon during the slack water of low tide.

8. The concentration of the oxygen at the surface showed a gradual tendency to decrease during the hours between sunset and sunrise.

9. High oxygen concentrations were obtained at the surface during periods of sunlight, the maximum conditions being obtained near the peaks of the two highest tides. However, in contrast with this, minimum concentrations of oxygen at a depth of 3.5 meters were obtained near the peaks of the two highest tides.

10. When decided decreases of oxygen were being noted at the surface during the first few hours of the tests, a corresponding increase in the oxygen concentration was being observed at a depth of

TABLE 1. *Hourly variations in temperature, dissolved oxygen and salinity (as chlorine) over a 25 hour period, at surface (S) and at depth of 3.5 meters (D); off the Puget Sound Biological Station, August 12-13, 1926.*

Time	Temperature °C		Dissolved oxygen per liter				Grams of chlorine			
			milligrams		milliliters		% saturation†		per liter S	per kilo. S
	S	D	S	D	S	D	S	D		
8:00 P.M.	12.3	12.0	7.77	6.18	5.44	4.33	88	69	17.25	16.89
9:00 P.M.	11.9	11.4	7.64	6.15	5.35	4.31	86	68	17.25	16.89
10:00 P.M.	11.4	11.2	7.25	6.30	5.08	4.41	81	69	17.33	16.96
11:00 P.M.	11.5	11.4	7.17	6.58	5.02	4.61	80	73	17.29	16.93
12:00 P.M.	11.5	11.5	7.29	7.13	5.10	4.99	81	79	17.25	16.89
1:00 A.M.	11.5	11.5	6.85	6.85	4.80	4.80	76	76	17.25	16.89
2:00 A.M.	11.5	11.5	7.01	6.85	4.91	4.80	78	76	17.25	16.89
3:00 A.M.	11.5	11.5	6.96	6.62	5.57	4.63	78	74	17.21	16.85
4:00 A.M.	11.5	11.5	6.69	6.75	4.68	4.73	78	75	17.21	16.85
5:00 A.M.	11.6	11.5	6.97	6.45	4.88	4.52	78	72	16.99	16.64
6:00 A.M.	11.6	11.5	6.74	6.65	4.71	4.66	75	74	17.17	16.81
7:00 A.M.	11.5	11.0	6.93	6.65	4.85	4.66	77	73	17.17	16.81
8:00 A.M.	11.8	11.5	6.65	6.38	4.66	4.47	74	71	17.15	16.79
9:00 A.M.	12.2	11.8	7.13	6.98	4.99	4.89	80	78	17.21	16.85
10:00 A.M.	12.5	11.7	6.90	6.90	4.83	4.83	78	77	17.15	16.79
11:00 A.M.	12.6	11.9	7.83	7.30	5.48	5.11	88	82	17.19	16.83
12:00 A.M.	12.6	12.2	7.52	7.42	5.26	5.19	85	83	17.25	16.89
1:00 P.M.	12.3	12.2	7.66	7.73	5.36	5.41	86	87	17.25	16.89
2:00 P.M.	12.0	11.8	7.66	7.78	5.36	5.45	86	87	17.25	16.89
3:00 P.M.	12.0	12.5	7.25	7.25	5.08	5.08	81	82	17.23	16.87
4:00 P.M.	12.3	12.1	7.66	7.25	5.36	5.08	86	81	17.21	16.85
5:00 P.M.	12.2	12.2	7.76	7.58	5.43	5.31	88	85	17.23	16.87
6:00 P.M.	12.3	11.9	7.80	7.73	5.46	5.41	88	87	17.19	16.83
7:00 P.M.	11.5	11.9	7.92	6.58	5.54	4.61	88	73	17.16	16.80
8:00 P.M.	11.8	11.4	7.90	6.55	5.53	4.59	88	73	17.26	16.90

†The term "saturation" refers to a condition of equilibrium between the solution and the oxygen pressure of the atmosphere. This pressure is 188.8 mm.

3.5 meters. This probably resulted from a mingling of the waters, a tendency also indicated by the curves for temperature and salinity.

11. The actual effect of sunlight upon the dissolved oxygen is further shown by a study of the per cent saturation for the sea water as illustrated in figure 5.

Sea Water of Argyle Lagoon and Argyle Channel

In table 2 are given the analyses of the waters of Argyle Lagoon taken at the surface and at the bottom (3.5 meters) together with the analyses of the waters of Argyle Channel during an ebbing tide. In order to study the water during a high tide, when there was a flow into Argyle Lagoon, a week had to elapse before the proper tidal conditions could be obtained which would permit daylight work. Table 3 gives the data collected at a high tide. The samples which furnished the data given in table 3 were obtained from the same locations which supplied the data for table 2. On the left in figure 4 are illustrated the data of table 2, while those of table 3 are shown at the right. From a study of these graphs and tables the following facts are noted:

(a) While there is a noticeable difference in the salinity, no general conclusion as to the possible effect of dilution may be drawn. The variation in the salinity between ebbing and flooding conditions is less than that shown in figure 3 for the 25 hour test for tidal changes.

(b) The water of Argyle Channel is practically the same as that on the surface of the lagoon during an ebbing tide. However, there is a noticeable difference between the surface water of the lagoon and that of the channel when the tide is flooding.

(c) For the ebb tide the peculiar situation shown by the lesser salinity at the bottom than at the surface is due to the effects of evaporation and temperature changes. Calculations from Knudsen's Hydrographical Tables show that the bottom water, owing to its lower temperature but with a salinity less than at the surface, has the greater density.

(d) The temperature of the waters is several degrees higher both for ebb and flood conditions in the lagoon than that shown in figure 3. The maximum temperature of the sea water at the Biological Station was 12.6° with a minimum of 11.2° . In contrast to this are temperatures of 18.3° and 14.0° for the ebb tide and 17.8° and 15.6° for the flood tide in Argyle Lagoon. From the latter observation it may be concluded that the temperature of the water is

TABLE 2. *Analyses of the waters of Argyle Lagoon during an ebbing tide, August 10, 1926.*

Time	Temperature °C	pH	Oxygen			Salinity, grams Cl.	
			mgm.	ml.	% sat.	per liter	per kilo.
Bottom lagoon							
9:30 A.M.	14.5	8.6	7.01	4.91	83	17.08	16.73
11:30 A.M.	15.2	8.6	8.91	6.24	106	17.10	16.75
2:00 P.M.	14.8	8.6	9.60	6.72	114	17.12	16.76
3:30 P.M.	15.2	8.4	9.85	6.90	117	17.14	16.78
5:00 P.M.	15.1	8.4	9.72	6.80	116	17.12	16.76
Surface lagoon							
9:45 A.M.	16.4	8.4	10.67	7.47	129	17.11	16.76
11:15 A.M.	16.6	8.6	11.81	8.27	146	17.14	16.78
2:15 P.M.	17.1	...	12.99	9.09	161	17.20	16.84
3:45 P.M.	18.3	8.6	12.97	9.08	163	17.17	16.81
5:15 P.M.	17.7	8.6	13.40	9.38	169	17.16	16.80
Center channel							
10:00 A.M.	16.4	8.5	11.92	8.34	145	17.14	16.78
11:30 A.M.	17.0	8.6	17.14	16.78
2:30 P.M.	17.8	8.6	11.30	7.91	142	17.20	16.84
4:00 P.M.	17.3	8.6	11.77	8.24	146	17.16	16.80
5:30 P.M.	14.0	8.6	11.03	7.72	129	17.16	16.80

TABLE 3. *Analyses of the waters of Argyle Lagoon during a flood tide, August 16, 1926.*

Time	Temperature °C	pH	Oxygen			Salinity, grams Cl.	
			mgm.	ml.	% sat.	per liter	per kilo.
Bottom lagoon							
10:30 A.M.	16.0	8.6	9.28	6.50	113	17.35	16.98
12:00 A.M.	15.9	8.4	9.76	6.83	119	17.35	16.98
2:00 P.M.	16.1	8.6	10.43	7.30	127	17.37	17.00
3:30 P.M.	16.2	8.6	10.67	7.47	129	17.35	16.98
Surface lagoon							
10:30 A.M.	16.2	8.6	10.67	7.47	130	17.29	16.93
12:00 A.M.	16.5	8.6	10.81	7.57	133	17.29	16.93
2:00 P.M.	17.3	8.6	11.07	7.75	136	17.31	16.95
3:30 P.M.	17.4	8.6	11.15	7.81	137	17.35	16.98
Center channel							
11:00 A.M.	15.7	8.4	9.28	6.50	108	17.35	16.98
12:30 P.M.	15.6	8.4	9.94	7.95	118	17.37	17.00
1:30 P.M.	17.2	8.6	11.34	7.94	139	17.35	16.98
3:30 P.M.	17.8	8.6	11.18	8.81	140	17.37	17.00

increased as it flows into Argyle Bay and still further raised after flowing through the channel into the lagoon.

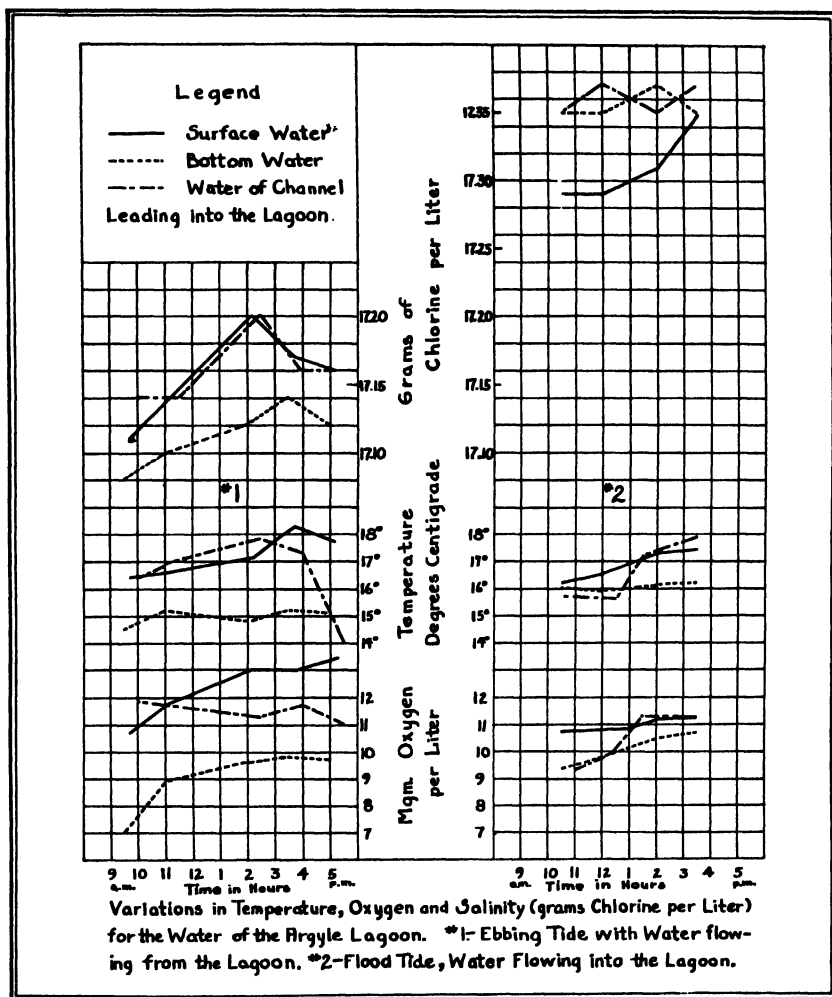


FIGURE 4

(e) The dissolved oxygen in the channel and at all places in the lagoon is very much greater than that found in the sea water of the Biological Station.

(f) The amount of dissolved oxygen in the channel and at the surface of the lagoon is considerably greater during conditions of an ebb tide than for a flood tide.

(g) The dissolved oxygen concentration of the waters at the bottom of the lagoon is less for ebb tides than for flood tides. A

study of the data indicates that a certain amount of dissolved oxygen is consumed at the bottom of the lagoon.

(h) For conditions at ebb tide it will be noted that a change took place at about 3:30 P.M. This marked change was due to a reversal of tidal conditions when water started to flow through the channel into the lagoon. By 5:00 P.M. when the next sample was taken, there was a very strong current of water flooding the lagoon and the changes that occurred are readily noticeable.

(i) The effect of light in promoting photosynthesis is readily seen from the steady increase in the concentration of the dissolved oxygen.

(j) The pH for the waters of Argyle Lagoon varied between 8.4 and 8.6 while that of the sea water off the Station varied from 8.0 to 8.2. (The pH data given herein are not corrected for the salt error).

Figure 5 shows the per cent saturation of the dissolved oxygen which was calculated from Whipple and Whipple's table.⁵ In the case of the sea water from the Biological Station complete saturation was never obtained, although the effect of actinic light is readily seen by a glance at the graph. In all cases, with the exception of the sample taken at 9:30 A.M. from the bottom of the lagoon during an ebbing tide, conditions of supersaturation were found in the waters of the channel and the lagoon. The samples from the surface during the ebb tide showed the highest supersaturation.

The increase in oxygen is undoubtedly due to the eel grass, *Ulva*, algae and diatoms present in the lagoon and the shallow waters of Argyle Bay.

In table 4 are given the data from a study of samples of water taken during an ebb tide at 4:00 A.M., August 17, 1926. Changes in temperature and the dissolved oxygen are the principal conditions that are subjected to change during the hours of darkness.

TABLE 4. *Analyses of water collected at 4:00 A.M. in Argyle Channel and from surface and bottom of Argyle Lagoon.*

Location	Temperature	pH	Oxygen		Per cent saturation	Chlorine	
			mgm per liter	ml per liter		gm per liter	gm per kilo.
Channel	16.0	8.6	8.40	5.88	102	17.33	16.96
Surface	16.2	8.6	10.91	7.64	132	17.31	16.95
Bottom	15.0	8.6	8.07	5.65	95	17.33	16.96

⁵ Standard Methods of Water Analysis, Am. Publ. Health Assoc., p. 62, 6th ed.

HYDROGEN SULFIDE

In portions of the lagoon where organic silt comprised the floor of the lagoon, very strong odors of hydrogen sulfide were noted upon digging into the material at low tide. In other portions of the floor of the lagoon the odor of hydrogen sulfide could be detected occasionally. However, no positive tests for the substance could be obtained in the water either quantitatively with .01 N iodine or qualitatively with Fisher's reagent.

The hydrogen sulfide was undoubtedly formed by the action of bacteria. The substance was detected in small amounts from the

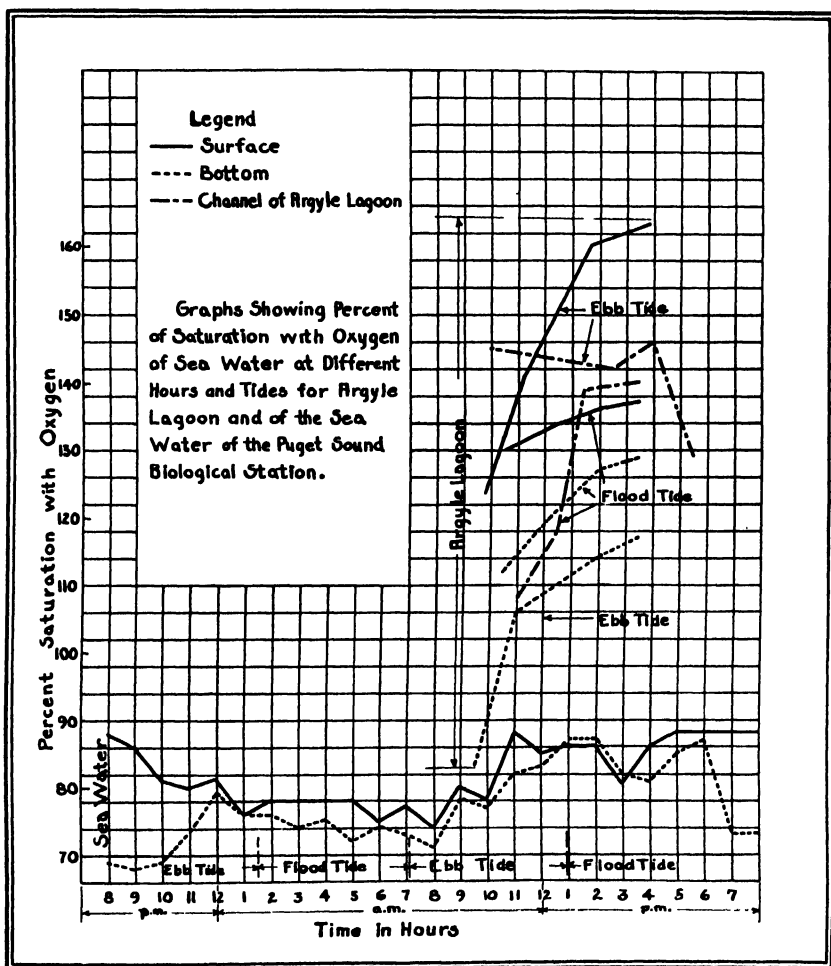


FIGURE 5

gases that bubbled from the lagoon at certain times. The high concentration of the dissolved oxygen, however, rapidly reacted with any of the hydrogen sulfide going into solution. The conditions favoring the formation of the hydrogen sulfide appear to be (a) an anaerobic condition, (b) organic matter, (c) sulfates, and (d) a definite concentration of sea water.

The occurrence of hydrogen sulfide in the Black Sea has been described by Zelinsky,⁶ Androussouf,⁷ Issatchenko,⁸ in the Lake Washington Ship Canal by Smith and Thompson,⁹ in sand and clay of the dunes of Holland,¹⁰ and in certain portions of bottom depths in contact with "blue mud" by Murray and Irvine;¹¹ hydrogen sulfide has been produced by bacteria taken from certain marine organisms by Newton.¹² It also has been noted by the writers in the silt and mud of various portions of the San Juan Archipelago. It is planned to make a more detailed study of the formation and presence of the hydrogen sulfide in organic silt exposed to sea water at a later date.

The constancy of the chloride-sulfate ratio has been shown by Thompson, Lang and Anderson.¹³ A variation of the ratio in the Lake Washington Ship Canal was noticeable due to the formation of hydrogen sulfide. In table 5 are given analyses of the waters of Argyle Lagoon for sulfates and chlorides.

TABLE 5. *Analysis of the waters of Argyle Lagoon.*

Date	Time	Gms SO ₄ per liter	Gms Cl per liter	SO ₄ Cl	Location in lagoon
8-16-26.....	4:00 P.M.	2.421	17.36	0.1395	Bottom
8-17-26.....	4:00 A.M.	2.437	17.39	0.1402	Bottom
8-17-26.....	4:45 A.M.	2.432	17.39	0.1399	Surface

The composite of the 50 samples of water from which the data in table 1 were secured on analysis gave 2.410 grams of sulfate (SO₄) and 17.26 grams chlorine per liter or a ratio of .1396. The waters of Argyle Lagoon show a slight deviation from the sulfate-chloride ratio for sea water.

⁶ J. Russ. Phys. Chem. Soc. 25: 298 (1893).

⁷ Guides des excursions du VII Cong. Geol. Internat. No. 29.

⁸ Compt. rend. 178: 2204 (1924).

⁹ Ind. Eng. Chem. 19: 822 (1927).

¹⁰ Proc. Konink. Acad. Wetensch. Amsterdam 25: 288 (1922).

¹¹ Trans. Roy. Soc. Edinburgh, 37: 481 (1895).

¹² Proc. Roy. Soc. Edinburgh, 21, 25 and 35 (1897).

¹³ Contrib. Can. Biol. 1: 379-399 (1922).

¹⁴ Thompson, T. G., Lang, J. W. and Anderson, Lucille. Publ. Puget Sound Biol. Sta. 5:277-292. (1927.)

CONCLUSIONS

1. The sea water of Argyle Lagoon during the summer months differs from the average sea water at the Puget Sound Biological Station in its higher temperature, greater concentration of dissolved oxygen and a slightly greater pH.
2. Differences between surface and bottom samples show a definite stratification of the water, even in these comparatively shallow depths. This is especially noticeable at or near the high tides.
3. The condition of the water in the lagoon is affected both by tidal changes and by local meteorological conditions; the influence of the latter predominate except at times of high tide.
4. The organic silt at the bottom of the lagoon contained quantities of hydrogen sulfide. The presence of the gas was not detected in the water.

The authors take pleasure in acknowledging the fact that it was Professor Trevor Kincaid of the Department of Zoology of the University of Washington who suggested this work, and desire to express their gratitude for his aid and advice during the investigation.

Studies on *Hormiscia Wormskioldii*

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Vassar College

Material was collected from the float at the Puget Sound Biological Station at Friday Harbor, Wash. Two lines of investigation were undertaken: (1) the determination of methods of killing, fixing and staining whole mounts; and the preparation of stained cross-sections; (2) the growing of young plants from the zoospores with the view of following the early stages of growth. The results will be discussed separately under these headings.

METHODS

Killing and fixing of material. Filaments of *Hormiscia* were first immersed for 24 hours in a solution of formalin-acetic-seawater made up in the following proportions: 10 cc of formalin, 5 cc glacial acetic acid, and 85 cc of seawater. Examination of the cells showed considerable shrinking of the protoplast from the cell wall. A second lot were then placed in a solution containing more acetic acid, in proportions 10-6-84. After 24, 48 and 96 hours no plasmolysis was visible. The material remained in this solution for one week or until practically colorless and was then washed with seawater.

Staining and mounting of whole material. A part of the material so prepared was again washed but in fresh water and stained with iron-haematoxylin, after which it was mounted in Venetian turpentine according to the methods outlined by C. J. Chamberlin (Methods in Plant Histology, Chicago, 1924, pp. 101-103). Another portion was stained with phloxine and aniline blue according to the magdala red-aniline blue procedure (Chamberlin, p. 105).

Preparation for sectioning, staining of sections. The remainder of the material killed was passed through the following series of alcohol in seawater: 2½ per cent, 5 per cent, 10 per cent, 20 per cent, 30 per cent, 40 per cent, 50 per cent, 70 per cent, 85 per cent, 95 per cent, 100 per cent. It remained in each for 24 hours. From the absolute alcohol it passed through the following concentrations of alcohol in xylol: 2½ per cent, 5 per cent, 10 per cent, 15 per cent, 25 per cent, 35 per cent, 50 per cent, 75 per cent, 85 per cent, 100 per cent. Infiltration with paraffin and imbedding in pure paraffin

were carried on according to Chamberlain's direction (p. 112). Sections were cut 3 microns in thickness and fixed upon slides with Mayer's fixative (Chamberlain, p. 118). After removal of the paraffin from the sections with xylol, they were stained with iron-haematoxylin (Chamberlain, p. 45) and mounted in balsam.

Discussion. Although some cells in the mounts showed a certain amount of plasmolysis, there were many more showing no trace. Observations were made upon these latter. Cross sections of the filaments showed the protoplast to be parietal, the major portion of such mature cells being occupied by a large vacuole (Figs. 1, 2). Nuclei were readily distinguished both where iron-haematoxylin and where phloxine-aniline blue were used. Examination of a whole zoosporangium showed zoospores tightly packed within, each with its nucleus clearly stained and its cytoplasm faintly so (Fig. 3).

YOUNG STAGES

Growth of young plants from zoospores. On June 30, the bottoms of museum jars were covered with glass slides, sterile seawater added and some filaments of *Hormiscia* introduced. After 48 hours many zoospores from the zoosporangium having escaped and settled upon the slides, the filaments were removed. The jars were kept covered and partially immersed in running seawater so as to keep the young plants growing as nearly under normal conditions as possible. At frequent intervals a slide was removed and examined under a high power microscope, then returned to the jar. After a month the young plants seemed to be doing less well than at the start so traces of $\text{Ca}_3(\text{PO}_4)_2$ and of KNO_3 were added to the water. At this time also a second culture containing these same materials was started. On August 18 the entire lot of slides were transferred to bottles along with some of the culture solution in which they had been growing and sealed. They were shipped to Poughkeepsie, N. Y. and opened October 1, after which they were allowed to remain in partially uncorked bottles until December. This treatment proved unsatisfactory for growth and all cells not killed formed heavily-walled resting cells.

Discussion. The diagrams indicate that zoospores (Fig. 4) settled on the slides, lost their cilia (Figs. 5, 6) and then sent out germinating prolongations (Fig. 7). About this time the nucleus divided (Fig. 8) and then a cross-wall formed (Fig. 9). From this point on no regularity of division could be noted. These two cells divided and

redivided in various directions forming sometimes a straight body and more often a mass of cells or an irregularly branched mass (Figs. 10-20). Could experimental conditions have favored further growth it should have been possible to determine without doubt whether these cells all act as a sort of basal holdfast mass from which filaments are later sent up or whether one end might attach itself while the rest floats free. The evidence secured certainly seems to favor the former method. By the time a 4-celled stage was reached (Fig. 14), cells began to exhibit more than one nucleus and more irregularity of chloroplast, but at no stage was the coenocytic appearance of a mature cell visible. These young plants were quite different from the adult.

SUMMARY

1. *Hormiscia wormskioldii* may be successfully killed and fixed in a 10-6-84 solution of formalin-acetic-seawater. Immersion for one week will not be detrimental.

2. Standard methods may be employed for staining and mounting whole or for imbedding in paraffin, staining and sectioning.

3. It is possible to grow young plants of *Hormiscia* on glass slides. Best results are obtained when traces of $\text{Ca}_3(\text{PO}_4)_2$ and KNO_3 are added to the seawater in which they are placed.

4. Cell division in the early stages of growth is irregular so that masses of cells are formed rather than straight filaments, these cells presumably to act as basal holdfasts for filaments to be later developed.

5. Cells of the young plant become multinucleate at about the four-celled stage.

6. Under unfavorable conditions cells or cell masses with heavy walls develop.

I am indebted to Dr. T. C. Frye for suggesting the problem and to Dr. C. J. Chamberlain for advice and direction in connection with the histological technique.

PLATE 22

Magnification $\times 325$ unless otherwise stated.

1. Cross-section of filament of *Hormiscia wormskioldii*. $\times 114$
2. Cross-section of filament of *Hormiscia wormskioldii*. $\times 416$
3. Tightly packed zoospores (in zoosporangium). $\times 416$

In seawater

4. Zoospore at time culture was started.
- 5-6. 48 hours old.
- 7-8. 66 hours.
9. 8 days.
- 10-12. 10 days.
- 13-15. 14 days.
- 16-18. 40 days. 10 days after addition of $\text{Ca}_3(\text{PO}_4)_2$ and KNO_3 .
- 19-20. 47 days. 17 days after addition of $\text{Ca}_3(\text{PO}_4)_2$ and KNO_3 .

In seawater containing a trace of $\text{Ca}_3(\text{PO}_4)_2$ and KNO_3 .

- 21-23. 7 days old
- 24-29. 18 days.
- 30-32. 126 days.

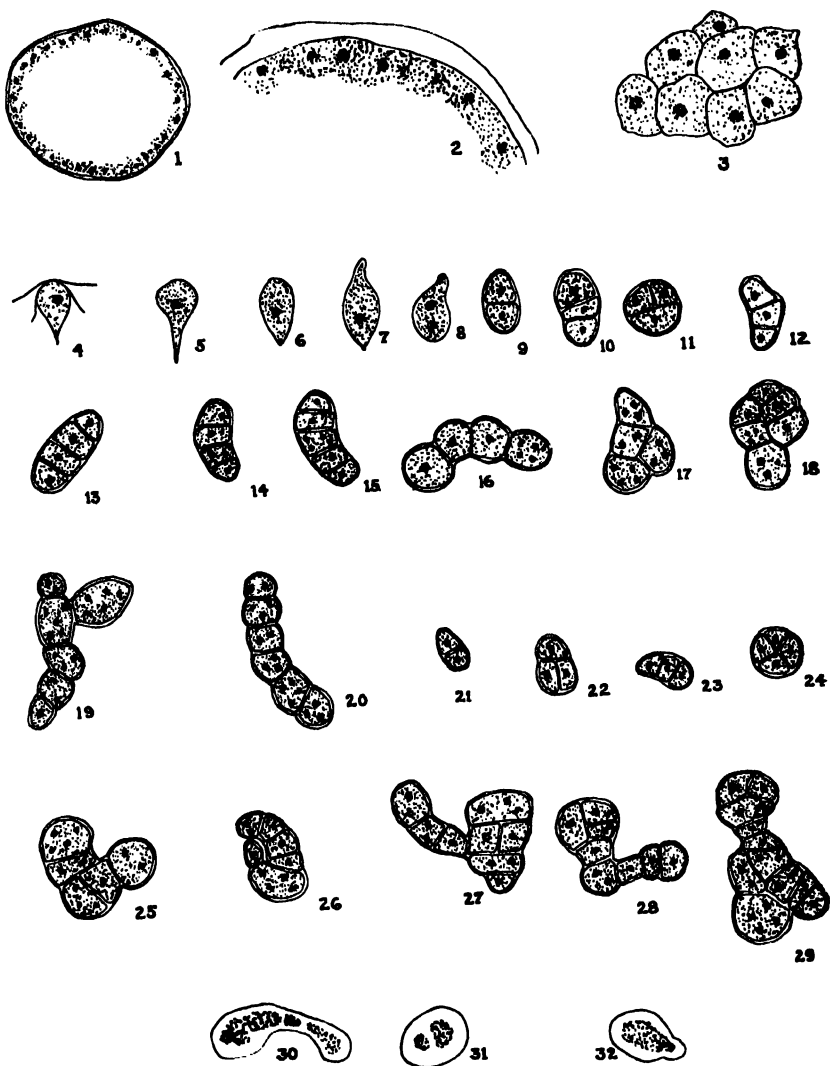


PLATE 22

A New Genus and Species of Sponge From Puget Sound¹

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Oberlin College, Oberlin, Ohio

The United States National Museum contains sponges collected by Miss Belle A. Stevens at Friday Harbor, Washington, that represent an interesting and novel type.

There are numerous sponge species (genera *Myxilla*, *Lissodendoryx*, etc.) which have a skeleton that is a pronounced polyspicular reticulum, having also chelas among the microscleres, and usually with special diactinal ectosomal megascleres. These are all characterized by the equi-ended chela. Species of sponge with anisochelas are also common, but usually associated with a skeleton of definite fibres, as for example in *Mycale*. The type under discussion at present is remarkable for the combination of reticulate structure with anisochelas.

Family DESMACIDONIDAE Vosmaer

Subfamily MYCALINAE Lundbeck

Genus BURTONELLA, gen. nov.

Main skeleton a polyspicular reticulation of monactinal megascleres; microscleres anisochelas, to which sigmas may be added. Known species has special diactinal ectosomal megascleres, and chelas of both the palmate and anchorate forms.

Burtonella melanokhemia, sp. nov.

Description. Amorphous in shape, fragile to spongy in consistency; usually in crusts less than 1 cm thick, but sometimes in masses nearly 4 cm in diameter; color dark brown, almost black; surface minutely cavernous; there are traces of a dermal membrane which perhaps covered the entire surface in life, and which contains a few dermal strongyles. In the parenchyma the protoplasmic tissues are much in evidence without any great quantity of spongin, but with many spicules; the chamber system is diplodal, the chambers close to 0.03 mm in diameter; the megascleres form a very conspicuous isodactyl reticulation, meshes usually triangular or rectangular. The skeleton is composed of : (1) abundant styles about 0.013 by 0.21 mm,

¹ This work was done at the Hopkins Biological Laboratory at Pacific Grove, California.

the main skeletal element; (2) a few smaller styles only 0.006 mm in diameter, with blunt ends spined; (3) a few dermal strongyles 0.01 mm, by 0.18 mm, ends slightly spined; (4) a few sigmas 0.05 mm long; (5) abundant anisochelas of great diversity in size and shape, 0.012 to over 0.04 mm, both anchorate and palmate chelas in the same individual; some of the smaller anchorate chelas lack the usual middle tooth; palmate chelas all of the larger sizes.

Locality.—Friday Harbor (Puget Sound), Washington, U.S.A.; on worm tubes, depth not stated.

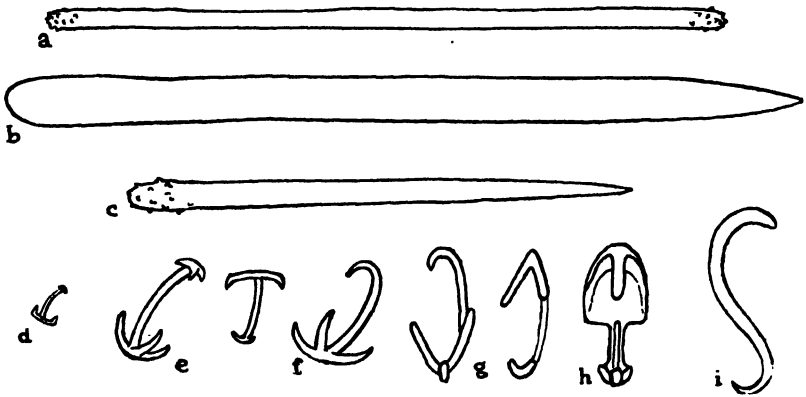
Holotype.—Cat. No. 21369 U. S. Nat. Mus.

The presence of anchorate and palmate chelas in the same individual is very unusual. The lack of small sizes in palmate ones, may possibly indicate that in this species the anchorate form develops into the palmate form. Among fresh water sponges the microcleres of the chela type (birotulates) develop in connection with gemmulation. It is possible that the chelas of marine sponges are similarly connected with some phase of the life history. I have found in *Ophalistaspongia pennata*² of the Pacific Coast that the chelas are sometimes present and sometimes absent. Do they first appear anchorate, and then become palmate? Practically the only difference between the genera *Myxilla* and *Lissodendoryx* is that the former has anchorate chelas and the second has other forms. Perhaps those species assigned to *Lissodendoryx* would have been *Myxillas* if collected during a different phase of their life history. The occurrence of the two types in *Burtonella* may be due to fortuitous circumstances as to its time of collection.

In color, and to a certain extent in structure this genus resembles the genus *Iophon*. It is like at least one species of *Iophon* in its unusual combination of palmate and anchorate anisochelas. *Iophon*, however, is sharply marked by the presence of very peculiar microcleres, the bipocilli.

The genus is named in honor of Mr. Maurice Burton of the British Museum (Natural History). The specific name is given in part because of the black color and in part because of the resemblance of certain spicule combinations in the slides of this specimen to the hieroglyph of a minor Egyptian deity, "Khem".

² The red sponges of Monterey Peninsula, California. Ann. Mag. Nat. Hist. S. 9, 19:265. 1927.

FIG. 1. *Burtonella melanokhemia*

a, Dermal strongyle; b, principal style; c, style with acanthose end; d, small two-pronged anchorate anisochela; e, f, various shapes of the anchorate anisochelas; g, side views of anisochelas; h, front view of palmate anisochela; i, sigma. All $\times 500$.

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The Rate of Oxygen Absorption by Certain Marine Fishes as Affected by the Oxygen Content and Carbon Dioxide Tension of the Sea-Water

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In earlier work (Powers, 1923), an attempt was made to determine the effect of the carbon dioxide tension of the seawater upon the rate of absorption of oxygen by the herring (*Clupea pallasii* Cuv. and Val.), during the first ten minutes of exposure. It was thought perhaps that this would throw some light upon the migratory and spasmodic movements of the herring. When the earlier experiments were performed on the herring (Powers, 1923) no rapid method for the measurement of the carbon dioxide tension had been developed. Thus the carbon dioxide tension could only be approximated. Now that a method has been developed (Powers, 1927 and 1928, and Powers and Bond, 1927, 1928) by which a rapid determination of carbon dioxide tension can be made, it was thought worth while to repeat the experiments, using herring (*Clupea pallasii* Cur. and Val.), silver salmon, or coho (*Oncorhynchus kisutch* Walbaum), and the viviparous perch (*Cymatogaster aggregatus* Gibbons), and include the effect of oxygen tension.

METHODS

The same methods were employed as in the earlier experiments (Powers, Fig. 1, 1923). Sea water of a given oxygen content and carbon dioxide tension from a five gallon glass bottle was passed over the fish which were contained in a quart or a half gallon fruit jar. The oxygen content and the carbon dioxide tension of the water were measured immediately before and after passing over the fish. The oxygen consumption was calculated in cc per kilo of fish per hour. There was always a slight error due to a use of a small amount of blood of the fish for determinations to be made on the blood. This error in the loss of weight of the fish was not corrected.

EXPERIMENTAL DATA

Herring (*Clupea pallasii*, Cuv. and Val.)

When table 1 is examined, it is seen that the rate of oxygen consumption in cc per kilo per hour is gradually reduced as the carbon

dioxide tension is raised. The oxygen consumption was lowered from 1,511 cc at 0.20 and 0.24 mm carbon dioxide tension to 82 cc at 13.27 to 17.40 mm carbon dioxide tension at ordinary oxygen content of the sea water. At low oxygen contents, 2.56 to 0.61 cc per liter, the fall of the rate of oxygen consumption is very much greater. When experiments 34 and 38, which have approximately the same carbon dioxide tension, are examined, it is found that the rate of oxygen consumption at the lower oxygen content is much less than at the higher oxygen content. When the data contained in table 1 are compared with data obtained in earlier experiments (Powers, table 1, 1923), there is agreement in the two sets of experiments. In the experiments in table 1 of this paper there is no correction for salt error for the reason given by Powers (unpublished), i.e., the error in calculating the carbon dioxide tension due to the salt error in reading the pH would be negligible and within the experimental error of the method. The lower pH readings recorded in the previous work were not due entirely to carbon dioxide tension of the water, but due to the addition of hydrochloric acid. Experiment 19 of the present work shows a low rate in the oxygen consumption, due either to experimental error or to low oxygen content of the water. The rate of oxygen consumption in experiment 32 indicates that the latter is the case. In the previous work the sea water in all experiments had a normal oxygen content. Experiment 36 shows a negative rate of oxygen consumption. It is conceivable that oxygen would be given off from the blood and tissues of the fish in this experiment, but this result is more apt to be due to experimental error.

Silver Salmon, or Coho (*Oncorhynchus kisutch*, Walbaum).

Table 2 shows the effect of carbon dioxide tension, low oxygen content of the sea water, and a combination of the two on the rate of oxygen consumption by the silver salmon, or coho salmon. In the high oxygen experiments the carbon dioxide tension did not run as high as in the experiments with the herring. Experiment 1 indicates that the optimum carbon dioxide tensions for oxygen absorption is a little above that of the partial carbon dioxide pressure of the atmosphere. The carbon dioxide partial pressure of the atmosphere at the Puget Sound Biological Station, during the summer, is generally from .22 to .23 mm.

Experiment 31 and all of the experiments with low oxygen contents of sea water show that the salmon are very susceptible to low oxygen content of the water.

Viviparous Perch (*Cymatogaster aggregatus*, Gibbons).

The data of the experiments showing the effect of carbon dioxide tension and oxygen contents of sea water, and a combination of these two factors (table 3) indicate that the viviparous perch is less susceptible to high carbon dioxide tension than either of the other two species of fishes tested. They show a more marked susceptibility to low oxygen than to high carbon dioxide tension, except where the carbon dioxide tension is very high, as in experiment 14. This is in keeping with observations by Powers (1922) and Powers and Logan (1925), showing that the alkali reserve of the blood plasma of the rock-fish and viviparous perch changes very rapidly with change in carbon dioxide tension of the sea water.

DISCUSSION

Observations recorded in this paper are not in opposition to the most recent findings in physiology. Evans (1926, page 54) says: "In other words, oxygen tends to displace carbon dioxide from the blood just as carbon dioxide is known to displace oxygen." Barcroft (1922) and other observers have shown that oxygen cannot be utilized at as rapid a rate with corpuscles at a lower per cent of oxygen saturation of the hemoglobin. Davies, Brow and Binger (1925) have found the respiratory response to carbon dioxide to be greater at high oxygen percentage than at low oxygen percentage of inspired air. Koehler and Reitzel (1925) have found an optimum pH for the rate of oxygen consumptions of minced muscle and liver. These last two may or may not have a direct bearing upon our findings. Our work is in agreement with that of Pereira (1924) if we assume that his hydrogen-ion concentrations of the sea water were due to carbon dioxide tensions.

SUMMARY

1. The rate of oxygen absorption in cc per kilo per hour during the first ten minutes of exposure, by the herring, (*Clupea pallasii*), by the silver salmon, or coho (*Oncorhynchus kisutch*), and by the viviparous perch (*Cymatogaster aggregatus*), is lowered by a decrease in the oxygen content or by an increase in the carbon dioxide tension of the sea water in the order named.

2. A combination of these two factors is more effective than either one alone.

3. The data seem to indicate that the herring is more sensitive to an increase in the carbon dioxide tension of the sea water, and the

silver salmon, or coho, is more sensitive to a decrease in the oxygen content of the sea water.

4. The viviparous perch is more resistant to changes in these two factors than either of the other two fishes.

5. This is in keeping with the fact that the alkali reserve of the blood plasma of the viviparous perch changes very rapidly with change in carbon dioxide tension of the sea water.

The authors wish to thank Professor T. C. Frye, Director of the Puget Sound Biological Station, for rooms, equipment, and materials for this work, and for many courtesies during its progress. The authors wish also to thank the University of Tennessee for the use of apparatus and materials.

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1928. Powers, E. B. The behavior of sea water, lake water and bog water at different carbon dioxide tensions. *Publ. Puget Sound Biol. Sta.* Vol. 6.

TABLE 1. Showing oxygen consumed in cc per kilo per hour by the herring (*Clupea pallasii*, Cuv. and Val.) at various carbon dioxide tensions and oxygen contents of sea water

No. of fish	No. of exptmt.	Tempera- ture C.	pH of water		Carbon dioxide tension of water in mm		Oxygen in cc per liter		Oxygen consumed in cc per kilo per hour
			before	after	before	after	before	after	
			running over fish		running over fish		running over fish		
4.....	34	17.0	8.30	8.25	0.20	0.24	6.27	4.16	1511
4.....	19	17.0	8.40	8.05	0.25	0.35	6.00	3.27	479
4.....	11	17.5	6.65	6.63	3.12	4.23	7.22	5.01	399
5.....	15	16.0	6.60	6.59	9.08	8.63	6.96	5.48	181
8.....	21	12.0	6.39	6.37	12.93	17.16	4.97	4.73	182
4.....	13	15.0	6.37	6.40	13.27	17.40	5.57	5.36	82
7.....	38	17.0	8.38	8.23	0.24	0.32	1.61	1.23	276
6.....	32	14.0	8.30	8.26	0.25	0.35	3.23	2.56	184
4.....	25	19.0	8.00	7.88	0.44	0.73	0.67	0.61	52
2.....	40	17.5	7.68	7.60	0.67	0.71	1.25	0.67	17
2.....	36	18.0	7.03	7.00	2.33	3.49	1.81	2.35	-14

TABLE 2. Showing oxygen consumed in cc per kilo per hour by the silver or coho salmon (*Oncorhynchus kisutch*, Walbaum) at various carbon dioxide tensions and oxygen contents of sea water

No. of fish	No. of expt.	Tempera- ture C.	pH of water		Carbon dioxide tension of water in mm		Oxygen in cc per liter		Oxygen consumed in cc per kilo per hour
			before	after	before	after	before	after	
			running over fish	running over fish	running over fish	running over fish	running over fish	running over fish	
2.....	33	16.0	8.30	8.29	0.22	0.22	5.15	4.73	183
2.....	31	18.0	8.30	8.28	0.23	0.26	3.19	2.67	132
1.....	1	13.0	8.23	8.13	0.28	0.35	5.31	3.93	832
2.....	7	14.0	7.90	7.85	0.51	0.56	5.77	4.11	344
2.....	9	16.0	8.27	7.30	0.22	0.77	6.73	4.78	363
1.....	3	13.1	8.00	7.80	0.43	0.69	5.40	4.61	304
2.....	5	15.0	8.00	8.34	0.43	0.87	5.56	4.31	363
3.....	37	17.0	8.39	8.34	0.23	0.25	1.61	1.23	188
1.....	23	18.0	8.30	8.28	0.29	0.28	0.78	0.76	3
3.....	29	18.0	7.82	7.68	0.26	0.37	3.16	2.25	123
2.....	39	17.0	6.64	6.70	0.67	0.69	1.25	1.18	14
2.....	35	18.0	7.10	7.03	2.53	4.42	0.18	0.18	0
2.....	27	17.0	6.64	6.70	9.07	7.15	0.20	0.17	9

TABLE 3. Showing oxygen consumed in cc per kilo per hour by the viviparous perch (*Cymatogaster aggregatus*, Gibbons) at various dioxide tensions and oxygen contents of sea water

No. of fish	No. of expt.	Tempera- ture C.	pH of water		Carbon dioxide tension of water in mm		Oxygen in cc per liter		Oxygen consumed in cc per kilo per hour
			before	after	before	after	before	after	
1.....	2	14.0	8.23	8.20	0.26	0.54	5.27	4.69	744
4.....	20	17.5	8.40	8.24	0.31	0.42	5.77	4.38	406
4.....	6	15.5	8.05	7.75	0.37	0.70	5.01	4.23	204
2.....	4	13.5	8.00	7.80	0.43	0.69	5.45	4.35	574
4.....	8	15.0	8.20	7.30	0.23	1.99	5.72	4.91	194
4.....	10	16.0	7.50	7.44	0.81	1.60	7.09	5.72	463
4.....	12	18.5	6.65	6.62	3.12	7.77	7.36	7.33	200
4.....	14	15.5	6.50	6.34	12.73	14.84	5.92	5.70	68
4.....	24	18.0	8.30	8.28	0.28	0.27	0.79	0.69	25
4.....	26	20.0	8.00	7.90	0.44	0.67	0.67	0.62	26
4.....	30	18.0	7.82	7.66	0.60	0.88	3.16	2.59	184
4.....	28	16.0	6.64	6.70	9.07	6.45	0.20	0.15	14
4.....	22	13.5	6.39	6.30	13.90	19.20	3.12	2.77	114

The Carbon Dioxide Tensions of the Fraser River and its Lower Tributaries and of Certain Tributaries of the Columbia River

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Observations recorded in this paper were undertaken to determine whether or not a characteristic difference could be found in carbon dioxide tension in lake waters, waters in streams fed by lakes, and the waters of streams not draining lakes; and to supplement the data that had already been collected by the senior author (Powers 1928).

The temperature of the water was taken with a Fahrenheit thermometer and reduced to centigrade. The barometric pressure was taken with an aneroid barometer, and the carbon dioxide tension was calculated by the method of Powers (1927) and Powers and Bond (1927).

In table 1 is recorded temperature, pH, carbon dioxide tension of the water before and after aeration, date, and barometric pressure of the Fraser River and its lower tributaries, and of certain tributaries of the Columbia River. Observations are recorded in order as one passes from Vancouver to Osoyoos over the Okanogan-Cariboo Trail via Lillooet and Clinton, and then by way of Grand Forks, Cascade and Colville to Spokane and from Spokane to Yellowstone National Park via Mullan, Missoula, Livingston and Gardiner. A map, which could be published, showing the definite location of the stations, has not been found. The dates and barometric readings will assist in definitely locating the stations on any good map. Observations were made as near the junctions of rivers as possible, if not otherwise stated.

The carbon dioxide tensions recorded in table 1 were calculated according to the formula published by Powers and Bond (1927), and have not been corrected according to a later formula (Powers and Bond, 1928). The correction if made would merely tend to show a greater difference in the carbon dioxide tensions of lakes and rivers fed by lakes, and of rivers not fed by lakes.

The first observation on a small lake between Hope and Yale was made merely because it was a lake. It seemed to be without

outlet at the time. This was indicated by the high temperature and the low carbon dioxide tension which, as will be seen in the following observations, seems to be true of lakes and rivers draining lakes in general. Nine Mile Creek was taken as a typical mountain stream having a rapid fall, low temperature, apparently high carbon dioxide tension, and low pH.

The Fraser River, a few miles above Nine Mile Creek, had a higher temperature, a lower carbon dioxide tension, and a higher pH than Nine Mile Creek. Anderson River as far as the authors are able to find does not drain a lake; however, it had a comparably low carbon dioxide tension.

The Thompson River, at its mouth, had a higher temperature, a higher carbon dioxide tension, and a lower pH than the Fraser River just above the mouth of the Thompson River.

The Fraser River, near Lillooet, above the entrance of Cayoosh Creek, and below Bridge River, had a temperature of 18.8°C., a carbon dioxide tension of 1.00 mm and a pH of 7.45, or a lower temperature, a higher carbon dioxide tension and a lower pH than that of Cayoosh Creek.

The conditions at Cayoosh Creek and Lake Creek are sufficiently striking to warrant comment. Above the junction of the two creeks, Lake Creek is a clear stream draining Seton Lake which in turn drains Anderson Lake. As far as the authors were able to ascertain there were no streams flowing into Lake Creek above the point at which the observation was made, which was just above its entrance into Cayoosh Creek. Cayoosh Creek had a lower temperature, a higher carbon dioxide tension, and a lower pH than Lake Creek. Cayoosh Creek was turbid. This creek drains a small lake, which, according to topographic maps is at an altitude of 5,000 feet, and would have a much lower temperature than Seton Lake, or even Cayoosh Creek at lower altitude. The topographic maps show, and the turbidity of the water indicates, that Cayoosh Creek is fed by various mountain streams. If the lake that feeds Cayoosh Creek had a low temperature, and we have no reason to believe that it does not, and if Cayoosh Creek is fed by various mountain streams, which we have every reason to believe is true, these are sufficient to explain the high carbon dioxide tension of the water of Cayoosh Creek in comparison with the water of Lake Creek by the fact that water with an alkali reaction has a very much higher carbon dioxide absorbing capacity at lower temperature than at higher temperature, and that mountain streams in

general at least apparently have higher carbon dioxide tensions than other streams (Powers, unpublished).

Bridge River, a river without a lake, at least without a lake contributing any great portion of the water feeding the river, shows the characteristics of a mountain stream with a low temperature, high carbon dioxide tension, and a comparatively low pH. However, the apparent carbon dioxide tension of the water is not as high as the apparent carbon dioxide tension of the water of typical mountain streams. Compare the carbon dioxide tensions of the water of Bridge River with those of Nine Mile Creek, Cayoosh Creek, above Lake Creek, Kettle River at Grand Forks, B.C.; Wolf Lodge Creek and Coeur d'Alene River in Idaho; St. Regis and Packard Creeks at Saltese, Montana; Firehole River, above the falls, Yellowstone National Park.

Thompson River at the outlet of Kamloops Lake has a carbon dioxide tension of water lower than that of waters at the mouth of the Thompson River. In other words the Thompson River had in some way increased the carbon dioxide tension of the water between Kamloops Lake and its mouth. The high carbon dioxide tension of the water of the north and south branches of the Thompson River is not clearly understood since both drain lakes, especially since the south branch drains lakes with such low carbon dioxide tensions, Little Shuswap and Salmon Arm Lakes. There are copper mines on the Thompson River system. The high carbon dioxide tension might be due to contamination of these streams.

Kamloops Lake is a good illustration of how the carbon dioxide tension of the water is lowered by the interception of a lake. The colder water of the two rivers obviously sank below the warmer epilimnion, and the Thompson River was merely draining the well aerated surface water which had a lower carbon dioxide tension and a higher temperature.

Lakes with extensive areas as compared with outlet, had lower carbon dioxide tension of surface water, as Little Shuswap and Salmon Arm Lake System, Kelly, Swan, and Kalamalka Lake, Woods and Okanagan, Vaseaux, and North and South Osoyoos Lakes. Lakes like Kamloops and Yellowstone had extensive outlets as compared with surface, and had surface waters with higher carbon dioxide tensions. Salmon Arm Lake, which is in reality a blind end of the Shuswap Lake System, had a lower carbon dioxide tension than that of the partial carbon dioxide pressure of the atmosphere. This sample was taken in the late afternoon of a bright sunshiny day. Doubtless

the low carbon dioxide tension was due to photosynthesis by the fixed vegetation and plankton.

Mountain streams, not fed by lakes, as Nine Mile Creek, B.C.; Kettle River at Grand Forks, B.C.; Wolf Lodge Creek, Idaho; Coeur d'Alene River, Idaho; St. Regis and Packard Creeks at Saltese, Montana; and Gibbon River in Yellowstone Park, are all characteristic and comparable with the mountain streams of the Smoky Mountains which have been studied in detail by the senior author (Powers, unpublished).

The Thompson River System and Spokane River, sixteen miles above Spokane, are the most obvious outstanding exceptions to the general rule that rivers draining lakes have a comparatively low carbon dioxide tension. Coeur d'Alene Lake has a carbon dioxide tension of the surface water of 1.14 mm, which is a marked exception to the rule by the findings of other lakes. The finding of this lake warrants further study in order to determine the cause of the high carbon dioxide tension or at least an apparent high carbon dioxide tension of its surface waters. An epilimnion should have been well defined at this time, August 29. Wolf Lodge Creek and Coeur d'Alene River both have a very high carbon dioxide tension. Wolf Lodge Creek had a carbon dioxide tension of 2.00 mm, which was the highest carbon dioxide tension of any water tested. Wolf Lodge Creek and Coeur d'Alene River on the other hand were not as typical Mountain streams as Nine Mile Creek, B.C., and St. Regis and Packard Creeks, Montana. Shelford (1923 and 1925) and Coker (1925) have found typical mountain streams to have a lower pH than streams of the lower elevations, which is at least indicative of a high, or at least apparently high carbon dioxide tension. A few miles above the point at which Coeur d'Alene River was tested extensive mining mills are located in the water shed of this river. One is led to speculate on the effect of contamination on the carbon dioxide tension of streams.

Yellowstone and the Clark Fork of the Columbia Rivers had very low carbon dioxide tensions. These are verifications of the findings of Powers (1928) during the summer of 1923. The reasons for the low carbon dioxide tension of these two rivers are not well understood.

SUMMARY

1. Lakes and rivers draining lakes had in general a lower carbon dioxide tension, average .57, than rivers not fed by lakes, average 1.05 mm of Hg.

2. Typical mountain streams apparently had higher carbon dioxide tension than streams of the lower lands.

3. Certain streams, as the Clark Fork of the Columbia River and the Yellowstone River, had very low carbon dioxide tensions, the reasons for which are not well understood.

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TABLE 1. *Showing the carbon dioxide tensions of the waters of the Fraser river and its lower tributaries, and certain tributaries of the Columbia river, as well as certain other streams and lakes as observed between August 23 and September 2, 1927. Data in each column given in the order indicated in the heading of the column.*

PLACE	Temperature °C of water Date	pH of water	Carbon dioxide tension of waters of rivers not fed by lakes	Carbon dioxide tension of waters of lakes and rivers draining lakes	Atmospheric pres- sure in mm Carbon dioxide partial in mm of Hg
Small Lake, between Hope and Yale, B.C.	23.6° 8/23	7.58		0.82	748.3 0.21
Nine Mile Creek, between Yale and Spuzzum, B.C.	16.7° 8/24	6.75	1.28		752.6 0.21
Fraser River, 14 miles above Yale, B.C.	18.9° 8/24	7.48		0.59	753.1 0.21
Chapman's Spring, Chapman's, B.C.	11.9° 8/24	8.22		0.35	749.3 0.22
Anderson River, 36 miles from Yale, B.C.	16.4° 8/24	7.63	0.76		739.3 0.21
Thompson River, at Lytton, B.C.	20.0° 8/24	7.22		1.06	742.7 0.21
Fraser River, at Lytton, B.C.	18.6° 8/24	7.49		0.55	742.7 0.21
Fraser River, Lillooet, B.C.	18.8° 8/24	7.61		0.67	739.6 0.21
Seton Lake, Craig Lodge, Lillooet, B.C.	21.7° 8/25	7.67		0.62	738.9 0.20
Seton Creek, Lillooet, B.C.	21.7° 8/25	7.66		0.62	739.9 0.20
Cayoosh Creek, Lillooet, B.C.	14.4° 7/25	7.21	1.46		739.9 0.21
Cayoosh Creek, below Junction	18.3° 8/25	7.45		1.00	740.7 0.21
Bridge River, Lillooet, B.C.	11.9° 8/25	7.14	0.83		740.4 0.21
Fraser River, at rapids, Lillooet, B.C.	18.9° 8/25	7.68		0.68	740.4 0.21
Kelley Lake, Pavilion Mt.	15.8° 8/26	8.27		0.20	665.0 0.19
Thompson River, at Kamloops, Lake	19.4° 8/26	7.48		0.76	722.6 0.20

TABLE 1—Continued

PLACE	Temperature °C of water Date	pH of water	Carbon dioxide tension of waters of rivers not fed by lakes	Carbon dioxide tension of waters of lakes and rivers draining lakes	Atmospheric pres- sure in mm Carbon dioxide partial in mm of Hg
Kamloops Lake, at outlet	19.4° 8/26	7.48		0.76	722.6 0.20
N. Br. Thompson River, Kamloops, B.C.	15.0° 8/26	7.16		1.21	724.9 0.21
S. Br. Thompson River, Kamloops, B.C.	18.9° 8/26	7.34		1.13	724.9 0.20
Little Shuswap Lake between Kamloops and Salmon Arm Lk.	18.9° 8/26	7.25		0.97	224.4 0.20
Salmon Arm Lake, near Salmon Arm, B.C.	21.9° 8/26	8.70		0.06	723.9 0.20
Swan Lake, Vernon, B.C.	19.7° 8/27	8.44		0.21	721.4 0.20
Kalamalka Lake, Oyama, B.C.	21.9° 8/27	8.43		0.21	719.8 0.20
Wood's Lake, between Oyama, B.C. and Kelowna, B.C.	21.9° 8/27	8.43		0.21	719.8 0.20
Okanagan Lake, Kelowna, B.C.	22.8° 8/27	8.38		0.24	723.6 0.20
Okanagan Lake, 6 miles from Penticton, B.C.	22.2° 8/27	8.43		0.21	720.9 0.20
Dog Lake, Okanagan Falls, B.C.	21.4° 8/27	8.43		0.21	719.2 0.20
Vaseaux Lake, Okanagan Falls, B.C.	22.8° 8/27	8.45		0.21	720.3 0.20
S. Osoyoos Lake, Okanagan Falls, B.C.	22.2° 8/27	8.46		0.20	724.7 0.20
N. Osoyoos Lake, Okanagan Falls, B.C.	22.2° 8/27	8.45		0.26	724.7 0.20
Rock Creek, Rock Creek, B.C.	13.4° 8/28	7.58	0.91		702.1 0.20
Boundary Creek, Greenwood, B.C.	11.1° 8/28	7.47	0.90		690.4 0.20
Kettle River, Grand Forks, B.C.	19.4° 8/28	7.37	1.13		708.6 0.20
Christina Lake, Cascade, B.C.	20.6° 8/28	7.41		0.87	712.5 0.20

TABLE 1—Continued

PLACE	Temperature °C of water Date	pH of water	Carbon dioxide tension of waters of rivers not fed by lakes	Carbon dioxide tension of waters of lakes and rivers draining lakes	Atmospheric pres- sure in mm Carbon dioxide Value of "n of Hg
Kettle River, near Marcus, Wash.	18.9° 8/28	8.25		0.25	717.0 0.20
Columbia River, Marcus, Wash.	16.4° 8/28	7.64		0.66	716.0 0.20
Loon Lake, Granite Pt., Wash.	20.6° 8/28	8.43		0.17	688.1 0.19
Spokane River, 16 miles from Spokane, Wash.	19.1° 8/29	6.93		1.02	703.5 0.20
Coeur d'Alene Lake, 16 miles from Spokane, Wash.	20.0° 8/29	7.10		1.14	701.3 0.20
Wolf Lodge Creek, Wash.	13.8° 8/29	6.70	2.00		699.5 0.20
Coeur d'Alene River, Wash.	15.6° 8/29	0.77	1.38		699.8 0.20
St. Regis Creek, Saltese, Mont.	13.3° 8/29	7.17	1.24		671.8 0.20
Packard Creek, Saltese, Mont.	14.9° 8/29	6.73	1.01		671.8 0.20
Clark Fork of Columbia, Superior, Mont.	15.3° 8/30	8.44	0.19		688.3 0.20
Yellowstone River, near Liv- ingston, Mont.	13.3° 8/30	8.57		0.18	636.8 0.18
Gardner River, Yellowstone Nat. Park	13.2° 9/1	8.26		0.22	619.5 0.17
Gibbon River, Yellowstone Nat. Park	10.0° 9/1	7.05	1.14		570.5 0.17
Fire Hole River, Yellowstone Nat. Park	10.5° 9/2	6.88		0.99	576.6 0.17
Spring Creek, Yellowstone Nat. Park	10.0° 9/2	6.76	0.51		575.8 0.17
Yellowstone Lake, Yellowstone Nat. Park	13.0° 9/2	7.22		0.78	575.0 0.16
Yellowstone Lake, Yellowstone Nat. Park	14.4° 9/2	7.20		0.82	574.3 0.16
Yellowstone Lake, Yellowstone Nat. Park	14.4° 9/2	7.37		0.53	574.3 0.16

The Carbon Dioxide Tension, Oxygen Content, the pH and the Alkali Reserve of Natural Waters Mostly of the Western Portion of the United States

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Data reported in this paper were collected during the summer of 1923. The main object of the observations was to determine whether or not there is a constant difference or are constant differences in the waters of lakes, of rivers draining lakes, and of the waters of rivers not fed by lakes. The author had in mind the peculiar habit of the sockeye salmon which almost invariably choose a stream fed by a lake or lakes when a choice of streams is presented during their spawning migratory movements in fresh water.

Experimental work has been done on marine fishes (Shelford and Powers, 1915; Shelford, 1918; Powers, 1921, 1922a, 1922b and 1923), the results of which led the author to believe that a guiding factor or factors in the movements of the migratory fishes, other factors being equal, is associated with the physiology of respiration. However, he has never considered these as the only factors involved. More recent works (Shelford, 1923 and 1925; Pereira, 1924; Powers and Logan, 1925; Powers and Shipe, 1928), have all pointed in the same direction. In short, the carbon dioxide tension of the water affects the tension at which oxygen can be absorbed from the water by fishes. It affects or modifies the alkali reserve of the blood plasma of fishes, and it affects the rate at which oxygen is utilized, at least during the first 10 or 15 minutes of exposure of the fish. The author has shown elsewhere that the so-called more sensitive fishes are more affected by the above mentioned modifications in the conditions of the water than the so-called less sensitive fishes. Thus a sensitive fish perhaps would have a tendency to choose the water in its path of migration to which it was best adjusted at that particular time. Observations made on streams and lakes (Powers, unpublished, and Powers and Hickman, 1928) have only served to strengthen this belief. Discussion of these points will be found elsewhere.

METHODS

The procedure in collecting water samples and in determining their carbon dioxide tension is the same as that already described

by Powers (1928), and Powers and Bond (1927). LaMotte color standards and indicators were used in determining the pH of the unaerated and aerated water. The Winkler method was used in determining the oxygen content of the water. The method of McClendon (1917) was followed in determining the alkali reserve of the water. HCl of about 0.01 N was used, and the end point was taken as being 4.2 pH.

EXPERIMENTAL DATA

The temperature, pH, the carbon dioxide tension, the oxygen content and the alkali reserve of the waters of a number of rivers and lakes of western United States were determined and the results are recorded in table 1. The observations were made at the most convenient places along the auto highways at the locations given in the table. When possible the samples of water were collected about three feet below the surface and always without allowing contact with the air. If the highway happened to cross the stream, samples were collected by lowering a sampling bottle from the bridge into the middle of the stream. The temperatures of the natural water and the water after it had been aerated are given in the table. There was always an error in the determined carbon dioxide tension of the waters due to the differences in temperature of the unaerated and aerated water. No attempt has been made to correct this error. In a few samples of water collected in the northwest the determined oxygen contents are perhaps low due to the absorption of the iodine by silt which found its way into the collecting bottle. These are marked with an asterisk (*).

The observations are arranged in the order in which they were taken during an auto trip from Memphis, Tennessee, to the Puget Sound Biological Station and return. Any good maps of the States and British Columbia will enable the reader to locate the stations. The date on which an observation was made is always given.

The carbon dioxide tensions recorded in table 1 were calculated according to the formula published by Powers and Bond (1927), and have not been corrected according to a later formula (Powers and Bond, 1928). The corrections if made would only tend to show a greater difference between the carbon dioxide tensions of the waters of lakes and of streams not fed by lakes.

The alkali reserve in table 1 is the number of cc of 0.01 n. acid required to neutralize 100 cc of water, 4.2 pH being taken as the end point.

DISCUSSION

When the data are summarized it is found that the average carbon dioxide tension of lake water and of rivers draining lakes is lower than that of rivers not fed by lakes*, the average carbon dioxide tension of the former being 0.32 mm and of the latter being 0.70. The oxygen contents of the water were just the reverse, that of the former being 6.39 cc per liter and that of the latter 5.81 cc per liter.

There are a few marked exceptions to this rule. The Illinois River is classed as a river fed by a lake. But it has a higher carbon dioxide tension and a lower oxygen content than any river of its class. This is due no doubt to the large amount of organic matter thrown into this stream. The Ohio River at Mound City, Ill., and the Cumberland at Smithville, Ky., both showed a higher carbon dioxide tension than would be expected of streams of their sizes. The high carbon dioxide tension may have been due to local conditions. Other observations not yet published show that a city, through contamination, can materially raise the carbon dioxide tension of a stream. The Okaw River, New Athens, Illinois, apparently a much contaminated stream, showed a very high carbon dioxide tension, 2.95 mm. and a very low oxygen content, 2.82 cc per liter.

Yellowstone, Boulder, Jefferson, Missoula, Clark Fork of the Columbia, St. Regis, Pitt (Calif.) and McCloud Rivers all gave a carbon dioxide tension of the water below the carbon dioxide partial pressure of the atmosphere. The explanation of this is not clear. Yellowstone River, since it picks up water from hot springs, can be classed by itself. Waters from hot springs would have a tendency to boil off the carbon dioxide, and because of the high carbonate content would be able on cooling to take up large amounts of carbon dioxide, the main source being that of the waters with which it mixes. The Missoula and Pitt (Calif.) Rivers flow from high plateaux into mountain ranges. There are perhaps two factors in these two rivers which may tend to lower the actual carbon dioxide tension of their waters. First, average climatic temperatures of the plateaux may be higher than those of the mountains into which the rivers flow; and second, the mountain streams flowing into these rivers would naturally have a lower temperature than the larger rivers. Both of these factors would tend to lower the temperatures of the larger rivers. As a general rule the waters of large rivers have a higher alkali reserve than the waters of mountain streams. Thus the waters of large streams have a higher carbon dioxide holding capacity. The carbon

*The Tennessee, Cumberland, Ohio, Mississippi and Missouri Rivers are considered as rivers not fed by lakes.

dioxide capacity of water is increased by lowering its temperature. The smaller volume of mountain stream water with a smaller carbon dioxide content, coming in contact with the water of the higher streams with a higher carbon dioxide capacity which has been increased by having its temperature lowered, would bring about an actual lowering of the carbon dioxide tension and even average carbon dioxide content of the water of the larger stream.

Since the carbon dioxide tensions of fresh waters, as has been shown by these observations and those of Powers (unpublished and 1928), and Powers and Hickman (1928), are higher than the carbon dioxide partial pressure of the atmosphere, the explanation as to why the carbon dioxide tension of lake surface waters is lower than other fresh waters in general becomes a very simple matter. The surface lake water has merely given off its carbon dioxide during its prolonged contact with air.

The actual pH values of both unaerated and aerated water samples taken from mountain streams are lower than from other streams, and are in agreement with the findings of Shelford (1923 and 1925), Coker (1925), and Powers (unpublished). These are perhaps two reasons for lower pH values in mountain streams. First, carbonates and bicarbonates are generally at lower concentrations. the carbonates and bicarbonates are generally at lower concentrations. Second, if the streams are draining forest beds, the water will contain organic matter in solution which will tend to increase the acidity (Powers, unpublished).

SUMMARY

1. The carbon dioxide tension, oxygen content, the pH and the alkali reserve of natural waters mostly of the western portion of the United States were determined.
2. The waters of lakes and of rivers draining lakes, other things being equal, had a lower carbon dioxide tension and a higher oxygen content than the waters of rivers not fed by lakes.
3. Mountain streams in general had a lower pH than the streams of the lower lands.

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TABLE 1. *Giving data on the natural waters of the western portion of the United States. The data in each column are recorded in the same order as given in the heading of the column.*

PLACE	Temperature of water of air Date	pH and CO ₂ ten- sion of water after aeration	pH and CO ₂ ten- sion of lakes and rivers draining lakes Oxygen in cc per l.	pH and CO ₂ ten- sion of water of rivers not draining lakes Oxygen in cc per l.	Alkali reserve (see text)
Clark River, Paducah, Ky.	19.0° 20.0° 5/21	7.70 0.21		7.05 1.06 5.16	9.46
Tennessee River, Paducah, Ky.	18.5° 20.0° 5/21	7.75 0.21		7.20 0.67 5.31	10.54
Cumberland River, Smithland, Ky.	18.5° 22.5° 5/22	7.99 0.21		7.46 1.19 5.56	15.48
Ohio River, Smithland, Ky. (Above other two)	17.5° 22.5° 5/22	7.65 0.21		7.18 0.72 3.71	14.02
Ohio River, Mound City, Ill.	18.5° 14.0° 5/22	7.98 0.21		7.23 1.29 4.50	14.80
Okaw River, New Athens, Ill.	28.0° 21.5° 5/23	7.95 0.21		6.82 2.95 2.82	15.54
Missouri River, St. Charles, Mo.	17.0° 23.0° 5/24	7.92 0.21		7.58 0.48 5.32	32.34
Mississippi River, Grafton's Ferry, Mo.	17.0° 18.0° 5/24	8.30 0.21		7.81 0.67 6.16	23.00
Illinois River, Grafton's Ferry, Ill.	17.0° 18.0° 5/24	7.62 0.21	6.90 0.87 2.84		31.82
Missouri River, Rocheport, Mo.	17.5° 23.0° 5/26	8.08 0.21		7.59 0.70 4.77	30.60
Missouri River, Omaha, Nebr.	19.0° 24.0° 5/28	8.08 0.20		7.87 0.33 4.65	32.10
La Platte River, Ashland, Nebr.	28.0° 28.5° 5/29	8.15 0.20		7.92 0.35 4.83
Elkhorn River, Norfolk, Nebr.	22.0° 26.0° 5/30	7.95 0.20		7.52 0.58 3.39*	30.16

TABLE 1—Continued

PLACE	Temperature of water of air Date	pH and CO ₂ ten- sion of water after aeration	pH and CO ₂ ten- sion of lakes and rivers draining lakes Oxygen in cc per l.	pH and CO ₂ ten- sion of water of rivers not draining lakes Oxygen in cc per l.	Alkali reserve (see text)
Missouri River, Yankton, S.D.	20.0° 25.0° 5/31	8.00 0.20		7.68 0.43 4.50	29.25
South Fork Cheyenne River, Wasta, S.D.	21.0° 27.0° 6/1	8.03 0.20		7.90 0.27 1.61*	27.25
Rapid Creek, Rapid City, S.D.	13.0° 13.5° 6/2	8.23 0.20		8.20 0.22 5.60	27.40
Powder River, Arvada, Wyo.	18.0° 24.0° 6/3	7.95 0.19		7.95 0.88 3.27*	20.92
Clear Creek, Regis, S.D.	16.0° 25.0° 6/3	7.73 0.19		7.62 0.25 5.38	11.25
Littlehorn River, Hardin, Mont.	6/4				34.32
Bighorn River, Hardin, Mont.	16.0° 21.0° 6/4	7.95 0.19		7.78 0.29 4.72*	17.86
Yellowstone River, near Huntley, Mont.	15.0° 25.0° 6/4	7.79 0.18	7.78+ 0.19— 6.01		14.00
Yellowstone River, Big Timber, Mont.	10.0° 16.0° 6/5	7.79 0.19	7.79 0.19 6.39		12.08
Boulder River, Big Timber, Mont.	8.5° 16.0° 6/5	7.81 0.06		7.76 0.19 6.87	9.17
Jefferson River, Jefferson Island, Mont.	13.5° 20.° 6/6	7.98 0.18		8.20 0.11 5.96	20.31
Cable Creek, Cable, Mont.	14.0° 17.0° 6/7	8.10 0.18		7.87 0.32 6.28	30.00
Georgetown Lake, North of Anaconda, Mont.	14.0° 17.0° 6/7	8.60— 0.17	8.59 0.17 6.64		26.74
Stewart Mill Creek, Georgetown Lake (as above)	15.0° 17.0° 6/7	7.97 0.17		7.40 1.08 6.70	35.47

TABLE 1—Continued

PLACE	Temperature of water of air Date	pH and CO ₂ ten- sion of water after aeration	pH and CO ₂ ten- sion of lakes and rivers draining lakes Oxygen in cc per l.	pH and CO ₂ ten- sion of water of rivers not draining lakes Oxygen in cc per l.	Alkali reserve (see text)
Flint Creek, Georgetown Lake (as above)	7.0° 12.0° 6/7	8.00 0.17		7.67 0.42 5.86	14.49
River draining Georgetown Lake, (15 miles down)	12.0° 21.0° 6/7	7.87 0.18	7.85 0.19 6.57		14.49
Missoula River, 20 miles east of Missoula, Mont.	14.0° 12.0° 6/8	7.98+ 0.18		7.98 0.18 5.71	18.45
Clark Fork River, 5 miles above Superior, Mont.	13.0° 22.0° 6/8	7.80 0.19		7.62 0.30 6.38	10.93
St. Regis River, St. Regis, Mont.	10.0° 24.0° 6/8	7.35 0.19		7.40 0.17	6.91
Spokane River, near Spokane, Wash.	14.0° 24.5° 6/9	7.34 0.19	7.18 0.30 7.37		4.26
Columbia River, Vantage Ferry, Wash.	13.0° 16.0° 6/11	7.72 0.21	7.68 0.29 7.72		11.08
Teanaway River, between Ellens- burg and Cle Elum, Wash.	8.3° 12.0° 6/11	7.59 0.20		7.20 0.57 7.47	9.43
Cle Elum River, between Cle Elum and Easton, Wash.	9.5° 10.3° 6/11	7.23 0.20	7.22 0.21 7.24		5.20
Yakima River, between Cle Elum and Easton, Wash.	7.8° 10.3° 6/11	7.41 0.20	7.01 0.59 7.24		5.65
Keechelus Lake, Snoqualmie Pass, Wash.	9.0° 10.5° 6/11	7.05 0.20	6.98 0.31 7.86		3.08
Mountain Stream, Snoqualmie Pass, Wash.	4.0° 5.0° 6/11	6.80 0.21		6.62 0.22 8.21	2.01
Deming Creek, base of Snoqualmie Pass, Wash.	6.0° 9.3° 6/11	6.55 0.20		6.55 0.20 7.88	1.91
Capilano River (Marine Drive) Vancouver, B.C.	17.5° 23.5° 8/9	7.02 0.21		6.91 0.28 6.43	1.67

TABLE 1—Continued

PLACE	Temperature of water of air Date	pH and CO ₂ ten- sion of water after aeration	pH and CO ₂ ten- sion of lakes and rivers draining lakes Oxygen in cc per l.	pH and CO ₂ ten- sion of water of rivers not draining lakes Oxygen in cc per l.	Alkali reserve (see text)
Fraser River, New Westminster, B.C.	17.5° 12.0° 8/10	7.85 0.21	7.59 0.41 6.50		5.65
Coquitlam River, Coquitlam, B.C.	21.0° 22.0° 8/10	7.51 0.21		6.58 2.40 5.56	2.45
Pitt River, above Coquitlam, B.C.	18.0° 25.5° 8/10	7.10 0.21	6.79 0.33 6.57		2.04
Fraser River, near Hammond, B.C.	17.5° 22.0° 8/10	7.75 0.21	7.58 0.41 6.65		5.47
Nooksack River, Ferndale, Wash.	16.0° 14.5° 8/10	7.60 0.22		7.12 1.14 6.71	4.05
Skagit River, Mt. Vernon, Wash.	14.5° 28.5° 6/11	7.98 0.21	7.75 0.35 6.89		3.11
Stillaguamish River, Pacific Highway, Wash.	20.0° 26.0° 8/11	7.89 0.21		7.15 1.29 6.25	4.88
Snohomish River, Everett, Wash.		Tide Flooding			
Cedar River, Renton, Wash.	14.3° 21.0° 8/13	7.72 0.21		7.37 0.52 7.30	4.16
Nisqually River, near Tacoma, Wash.	15.5° 21.0° 8/14	7.72 0.21		7.13 0.95 6.97	3.63
Cowlitz River, near Oregon City, Ore.	20.0° 19.5° 8/14	7.60 0.21		7.15 0.80 6.38	3.95
Columbia River, 31 miles above Portland, Ore.	20.3° 20.5° 8/15	8.28 0.21	8.21 0.25 7.10		8.66
Sandy River, 25 miles above Portland (Columbia River)	19.0° 20.5° 8/15	7.71 0.21		6.82 1.37 6.70	3.33
Willamette River, Milwaukie, Ore.	18.0° 27.5° 8/15	7.87 0.21		7.37 0.72 7.00	4.33

TABLE 1—Continued

PLACE	Temperature of water of air Date	pH and CO ₂ ten- sion of water after aeration	pH and CO ₂ ten- sion of lakes and rivers draining lakes Oxygen in cc per l.	pH and CO ₂ ten- sion of water of rivers not draining lakes Oxygen in cc per l.	Alkali reserve (see text)
Santiago River, near Willamette River, Ore.	22.0° 29.0° 8/15			7.20 4.01	3.29
Willamette River, Albany, Ore.	22.5° 22.5° 8/15	7.86 0.20		7.18 1.78 6.55	4.07
Umpqua, North Fork, Roseburg, Ore.	20.3° 28.0° 8/16	7.87 0.20	7.41 0.64 6.32		4.21
Umpqua, South Fork, near Roseburg, Ore.	24.5° 31.5° 8/16	8.27 0.20		7.85 0.53 6.28	6.17
Rogue River, Grant's Pass Park, Ore.	20.5° 26.0° 8/16	7.88 0.19	7.82 0.22 7.26		5.85
Klamath River, near Gottville, Calif.	20.0° 29.5° 8/17	7.88 0.19	7.88 0.19		7.29
Pitt River, Baird, Calif.	19.0° 29.0° 8/17	8.23 0.20	8.23 0.14 6.88		9.88
McCloud River, at mouth Calif.	15.5° 19.0° 8/17	8.08 0.20	8.22 0.11 7.33		7.41
Sacramento River, Redding, Calif.	19.0° 20.0° 8/18	8.20 0.20	7.93 0.40 6.81		9.14
Salt River, Phoenix, Ariz.	31.3° 37.5° 3/23	8.48 0.19		8.21 0.36 6.19	34.58
Pecos River, Pecos, Texas	31.5° 30.0° 8/27	8.27 0.19		8.03 0.35 6.46	19.24
Colorado River, Austin, Texas	28.5° 27.5° 8/30	8.60 0.20		7.88 0.72 4.25	25.65

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CORRECTIONS

Page 33, line 8; "Introductcion" should be Introduction.

Page 35, line 11; "varioius" should be various.

Page 36, line -4; "zones" should be belts.

Page 35, line 3; "*curiosus*" should be *cariosus*.

Page 56, line 21; "*pugettensis*" should be *pugetensis*.

Page 59, line -7; "*Tricopterus cancellatus*" should be *Trichotropus cancellata*.

Page 59, line -5; "*pugettensis*" should be *pugetensis*.

Page 128, line -18; "CaHPO" should be CaHPO_4 .

Pages 143 and 145; interchange the descriptions of the figures.

Page 178, line -12; between "2:" and "1169" put 3:.

Page 224, line 20; "gavinac" should be vaginae.

Page 234, line 11; "solut ons" should be solutions.

Page 238, line -11; "One tenth" should be One-tenth.

Page 243, line -10; "Straburger" should be Strasburger.

Page 247, line -5; "*minimum*" should be *minimus*.

Page 248, line 6; "incine" should be incline.

Page 253, line -2; "developd" should be developed.

Page 254, line 20; "injections" should be injections.

Page 255, line -13; "poist" should be moist.

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The Liverworts of the Northwest

LOIS CLARK and T. C. FRYE

University of Washington

Received for publication March 14, 1928.—Editor.

The detailed work herein covers chiefly the liverworts of the state of Washington, since the work was carried on for years with the idea of limiting it to that state. It was finally decided that it would prove more useful if other states were included. Thus it covers the states of Washington, Oregon, Idaho, Montana and Wyoming. However for this area, other than Washington, it chiefly brings together the facts published or otherwise secured, usually without the material at hand for study. All locality references are to Washington unless otherwise stated. Naturally, errors may be expected; it would be astonishing if there were none. Perhaps this account may be a stimulus to some one to write a better one. This is a complete list of the liverworts of the states mentioned above so far as we are aware. It is expected that others will be found; and it is hoped this work will stimulate collection.

It is intended that the work on the liverworts be used in conjunction with MacVicar's Student Handbook of British Hepatics, second edition, 1927; 24 shillings; Weldon & Wesley, 3, Arthur St., New Oxford Street, London, W.C.2, England. Only those not figured in his book are here illustrated. The British volume contains a surprisingly large per cent of our western hepatics.

It is believed that tabular comparisons will prove to be more useful than keys for they consider the same facts for all of the members, while keys do not, specially when a large number of members are to be separated. The comparisons are so arranged that they constitute keys.

A uniform ending for families (-aceae) and for orders (-ales) makes for clarity, and these are therefore thus used only.

The bryophytes form a distinct, clearly defined subkingdom or phylum in the plant world, occupying a position between the thallophytes (mostly algae and fungi) and the pteridophytes (fern group).

It is customary to divide the group into two classes, the hepaticae (liverworts) and the musci (mosses). Only the hepaticae are herein treated.

Thalloid liverworts are at once distinguished from mosses by the leafiness of the latter; but the leafy liverworts are not so easily recognized. Nearly all leafy liverworts are complanate, have veinless leaves, and have nearly isodiametric leaf cells; a moss may have one or two

- AA. Elaters present, with spiral thickenings; pores when present greatly modified; capsule not imbedded in the thallus, with a stalk. *Marchantiaceae*, p. 10

Comparison of families of Marchantiales	Ricciaceae p. 4	Marchantiaceae p. 10
Elaters none or with spiral thickenings.....	n	s
Sporophyte with stalk.....	—	+
Sporophyte sunken in gametophyte.....	+	—
Capsule rupturing the archegonium at maturity or not rupturing it at all.....	n	r
Sex organs sunken in the thallus; or only archegonia or both sexes on stalked receptacles.....	s	a b
Pores when present with greatly modified cells about them.....	—	+
Air chambers when present containing greatly modified photosynthetic cells.....	—	±

Family R I C C I A C E A E

Gametophyte a fleshy dichotomous thallus, rarely subsimple; dorsal surface with midrib; air chambers enclosed in the chlorophyll layer, narrow, conspicuous, vertical, canal-like, rarely large chambers, not containing specialized tissue; pores rudimentary or rarely well developed; ventral scales present or obscure; antheridia and archegonia sunken on dorsal surface just back of the growing point; archegonial neck exserted; androecium a cavity; osteoles conic-cylindric, elevated; sporophyte a capsule without a foot or stalk, enclosed in a calyptra; capsule wall thin, early broken down; spores at maturity free in the calyptra; elaters none.

- A. Pores either none or not surrounded by special cells; air chambers none or present; antheridia scattered in the dorsal surface of the thallus. *Riccia*, p. 5
- AA. Pores present, surrounded by special cells; air chambers present; antheridia in the ridge within the double furrow of the thallus. *Ricciocarpus*, p. 9

Comparison of species of Ricciaceae	Riccia					Ricciocarpus natans p. 9
	5. beyrichian:	1. fluitans	2. crystallina	3. frostii	4. sorocarpa	
Margin of thallus ciliate but sometimes only near tip.....	+	-	-	-	-	-
Scales of thallus white or violet.....	w-v	w	w	w	w	v
Antheridia scattered or in median furrow ..	s	s	s	s	s	f
Pores distinct, small or none.....	n	s	s	n	n	d
Costa carinate, reduced or none.....	c	c	c-r	n	n	r
Cross section of thallus flat, monoconvex, biconvex, subelliptical to oblong or subquadrate.....	m	b	b-q	c	q	fm
Thallus furrowed thruout or at apex only...	t	a	a	t	t	t
Furrow of thallus deep and narrow.....	-	-	-	+	+	+
Spores papillose.....	-	-	+	-	+	+
Thallus furrow acute.....	-	+	-	-	+	+
Diameter of spores in mu.....	75-130	65-104	60-110	46-65	65-100	42-57
Spores areolate or merely ridged or neither..	a	a	a	r	n	a
Tip of thallus subarcuate, obtuse, emarginate, or obcordate.....	s-c	o	o-c	o	s	o
Thalli monoicous or dioicous.....	m	m	m	d	m	m
Depth of thallus at thickest part as measured in cells.....				14-20	± 25	
Rhizoids pegged or smooth.....	s	s	s	s	s	ps
Dry thallus wrinkled or smooth.....	s	w			s	

RICCIA

Plants terrestrial or rarely aquatic; thallus forming more or less perfect rosettes, dichotomous, fleshy; lobes linear or cordate, bordered with median furrow; air chambers enclosed in the chlorophyll layer, narrow, subvertical, sometimes large, thin, breaking through the dorsal surface thus giving the thallus a torn appearance; ventral portion of costa composed of parenchyma cells with or without chlorophyll; central layer of costa indistinct, composed of parenchyma cells, starch-bearing; epidermal cells disintegrating and collapsing; pores rudimentary, surrounded by slightly differentiated epidermal cells; ventral scales hyaline, brownish or dark purple, conspicuous or fugaceous, arising from the ventral surface in a single row, later split along median line; dioicous or monoicous; sex organs scattered; capsule immersed; spores large, more or less tetrahedral; surface of spores

with free or mesh-like ridges, angles of areoles sometimes papillate, plane surface sometimes punctate.

A. Margin of thallus not ciliate.

B. Pores small; costa carinate; thallus furrowed at apex only.

C. Usually floating; thallus segments long and narrow, dorsal surface never lacunose. 1. *R. fluitans*

CC. Not floating; thallus segments broadly triangular, dorsal surface of older parts lacunose. 2. *R. crystallina*

BB. Pores none; thallus furrowed thruout.

D. Furrow of thallus obtuse; thallus subelliptical in cross section, dioicous; spores 46-65 μ in diameter, ridged.

3. *R. frostii*

DD. Furrow of thallus acute; thallus subquadrate in cross section, monoicous; spores 65-100 μ in diameter, papillose.

4. *R. sorocarpa*

AA. Margin of thallus few to many ciliate.

5. *R. beyrichiana*

1. *Riccia fluitans* Linne.

Thallus floating or creeping on soil, green, 1-5 cm long, repeatedly dichotomous; dorsal surface smooth, often wrinkled on drying, sometimes lacunose with age; root hairs wanting in water forms; main segments narrow; terminal segments oblong to linear, obtuse, emarginate, margins flat, 2 or 3 cells thick or more or less unistratose, furrow shallow at apex; scales rudimentary on land forms, deficient on water forms, violet in color; dorsal epidermis persistent, unistratose, disintegrating over air chambers when old; pores present in land forms, absent in water forms; cells .04-.09 mm in land forms, .05-.2 mm in water forms; air chambers large, unistratose lamellae present; monoicous; capsule in land forms only, forming slight elevations on ventral surface; spores yellow brown, translucent, .065-.1 mm in diameter, margined; areolae more or less smooth, larger ones enclosing a free-ending spur or tubercle; inner face with short free or anastomosing ridges.

On wet soil. Bellevue (Frye) 1921, (Daugherty) 1922; Tolt (Rigg), 1926; Tukilwa (Wells), 1928.

Oregon: Albany (Van Wert), about 1922.

Known from Colorado (16), British Columbia and California (39). It is likely more prevalent than the collections indicate.

2. *Riccia crystallina* Linne.

Plants 2-6 times dichotomous, forming rosettes 5-30 mm in diameter, thick, obcuneate, grayish green to dark green, crystalline when young, concolorous beneath; segments crowded, becoming spongy in appearance thru the disorganization of the epidermis; margin not ciliate; terminal segments 1-2.5 mm wide, obcuneate or obcordate; cross sections 2-4 times as wide as high, oblong to almost rectangular, dorsal and ventral surfaces nearly flat and parallel; air chambers large, elongate-polyhedral, separated by unistratose lamellae, in 2-4 vertical series; ventral scales none or obsolete; monoicous or rarely dioicous; spores yellowish brown to dark brown, .06-.11 mm, granulate papillose, often crenulate-cristulate, margin mostly .003-.01 wide, outer face somewhat imperfectly areolate; areolae .01-.045 mm wide, enclosing a free-ending spur or an isolated tubercle; older spores usually tuberculate-papillate in profile.

Oregon (9).

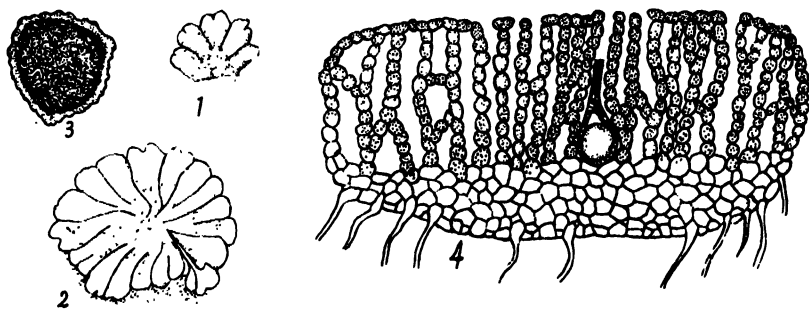
The collection mentioned above is the basis for its inclusion. We have not examined the material, and know of no other report of it within our area.

3. *Riccia frostii* Austin, Bull. Torr. Bot. Club. 6:17. 1875.

Riccia watsoni Austin, Bull. Torrey Bot. Club. 6:17. 1875.

Riccia beckeriana Stephani, Bull. Herb. Boiss. 6:374. 1898.

Thallus thin, pale or grayish green, closely appressed to substratum, in rosettes, 3-8 mm long, 3-4 times dichotomous, 15-20 cells thick in median line, attenuated to a unistratose margin; lobes again forked, .5-1.5 mm wide; dorsal surface fibro-reticulate and minutely



Riccia frostii. 1. Young plant, $\times 4$. 2. Plant, $\times 4$. 3. Cross section of lobe of thallus, $\times 50$. 4. Spore, $\times 240$. (1, 2, after Kephart; 3, 4, after K. Mueller).

pitted, becoming spongy and filled with cavities; air chambers large; ventral scales none or rudimentary; dioicous; capsules immersed, numerous, round; the epidermis covering them soon ruptured; spores light brown .045-.054 mm in diameter, narrowly margined; surface marked with numerous ridges; ridges wavy, rarely united; antheridial plants small, purple; antheridia immersed; ostioles slender, elevated, 1 mm long.

On silty deposits along rivers. Wawawai (Piper), 1895; Carley (Frye), 1908; Palouse River (Wells), 1926.

Idaho (33, 18).

Montana: Great Falls (18).

4. *Riccia sorocarpa* Bischoff.

Thallus small, 4-9 mm long, forming irregular patches, 1-4 times dichotomous, minutely regularly and compactly reticulate above; bright to light green; main segments oblong, terminal segments oblong, sub-acute, margins acute, naked, often hyaline and membranous, ascending, often incurved on drying, sometimes purple; furrow acute; scales small, whitish or hyaline, often reaching margin at the apex; transverse section subquadrate, 1-2 times as broad as thick, 25 cells thick in median portion; dorsal epidermis 2 or 3 cells thick, upper layer often forming persistent cups through thickening of lower portion of lateral walls and disintegration of portion; monoicous; capsules numerous; spores dark brown, .067-.1 mm, angular, papillate and crenulate; outer surface areolate; inner face densely and minutely punctate, or with very short numerous low ridges which do not form areolae.

On soil. Cascade Mountains (Frye), 1922; Flat Top Island in San Juan County (Else M. Frye), 1923.

5. *Riccia beyrichiana* Hampe, Lehm, Pugill. 7:1. 1838.

Riccia lescuriana Austin, Proc. Acad. Nat. Sci. Philadelphia 1869:232. 1869.

Riccia lesquereuxii Stephani, Bull. Herb. Boiss. 6:324. 1898.

Thallus .5-10 mm long, forming rosettes, 1-4-dichotomous, light green and reticulate above, green or tinged with red at margins beneath, sometimes subcarinate; main segments linear-obcuneate, sometimes nearly cordate; terminal segments ovate or oblong, more or less acute; margins abruptly ascending, often incurved on drying, usually with 1-2 rows of cilia; cilia obtuse or acute, sometimes curved, smooth

or granulate, .075-.3 mm long; furrow broad, flat bottomed in older portions, narrow and more or less closed by converging margins in younger portions; scales few, hyaline to whitish or sometimes red purple; transverse section of thallus 1-2 times as broad as high, concavo-convex; dorsal epidermis of 2 or 3 layers; cells of outer layer thin walled, ovoid, hemispherical or dome-shaped, disintegrating or leaving persistent cups; lower layers of large hyaline cells; monoicous; capsules immersed; thallus naked, often purple; spores brown, sometimes opaque, .065-.14 mm, mostly .075-.13 mm, angular, occasionally flattened, margin wanting or granulate or interrupted; outer face strongly areolate, smooth or papillate in side view; inner faces nearly smooth or rarely faintly and irregularly areolate.

On soil. Paradise Creek in Moscow, Idaho, (Clark), 1924.

Reported from British Columbia (21) and California (39), thus likely to occur in Washington and Oregon.

Evans mentions *R. michelii* as occurring in Montana and Idaho. Howe six years later does not include it among the North American species. We surmise that the plants may have been the nearly related *R. beyrichiana*. *R. michelii* is dioicous, and has the areolae of the spores .005-.007 mm wide; *R. beyrichiana* is monoicous, and has the areolae of the spores .01-.018 mm wide.

RICCIOCARPUS

Thallus Lemna-like, floating or stranded by drying of the pools, dark green thruout or purple margined, dichotomous, 2-4-lobed; lobes obovate or obcordate; dorsal surface deeply furrowed, ventral surface covered with long scales; scales numerous, linear or linear-lanceolate, dentate, reddish violet to nearly black, present chiefly in aquatic forms; rhizoids present in stranded forms, long, colorless, without peg-like inner projections, chlorophyll layer unistratose; air chambers large, irregular or polyhedral, separated by unistratose plates, ventral colorless layer reduced; epidermis with hexagonal areolae; areolae small but distinct; pores surrounded by 5-8 elongated cells; dioicous; archegonia sunken in two rows along the midrib; spores escaping thru the pores, black, round-tetrahedral; antheridia borne in elongated ridges; androecium in median furrow. The only known species is the following.

1. *Ricciocarpus natans* (Linne) Corda.

Compared with *Riccia* on page 5.

In marshes or at edges of ponds. Tacoma (Röll), 1888; Seattle (by ?), 1897; Kenneydale (Frye), 1907; Bellingham (Romine), 1907;

Hoquiam (Foster), 1908; Wallula Gorge (Frye), 1908; Burlington (Clark), 1911; Georgetown (Frye), 1911; Dungeness (Foster), 1913; Trout Lake on San Juan Island (Clark), 1923.

Oregon: Albany (Van Wert), about 1922.

Family **MARCHANTIACEAE**

Plants thalloid, thin or fleshy; dichotomous or innovating by ventral branches; costa more or less distinct; air chambers well developed in chlorophyll layer, often containing assimilating tissue or divided by chlorophyll-bearing cells into smaller chambers; pores present except in *Dumortiera*, which has not been found in our area, surrounded by barrel-shaped wall of several cells projecting into the lower tissue, or by four modified epidermal cells in the same stratum; sex organs usually on long-stalked differentiated receptacles; capsule short-stalked, breaking thru the calyptra at maturity, dehiscing irregularly or by a lid, rarely by valves; spores with sterile hairs or elaters.

- A. Stalked receptacles none; dorsal epidermis with trigones which bulge into the cells. *Targionia*, p. 12
- AA. Stalked receptacles present; dorsal epidermis without trigones large enough to bulge into the cells.
- B. Epidermal pores of the thallus simple; antheridia not on stalked receptacles.
- C. Air chambers without photosynthetic filaments.
- D. Stalk of female receptacle without furrow; wall of capsule with semiannular thickenings. *Clevea*, p. 13
- DD. Stalk of female receptacles with 1 furrow; wall of capsule without semiannular thickenings.
- DE. Female receptacle conic to hemispheric; spores 48-135 μ .
- F. Pseudoperianth none. *Reboulia*, p. 14
- FF. Pseudoperianth present. *Asterella*, p. 18
- FE. Female receptacle diskshaped; spores 30-50 μ . *Cryptomitrium*, p. 15
- CC. Air chambers containing photosynthetic filaments.
- G. Gemmae cups none; walls of capsule with semiannular thickenings; spores 70-90 μ ; female receptacle conic, its stalk with 1 furrow. *Conocephalum*, p. 23

Comparison of genera of Marchantiaceae		Marchantia, p. 26	Preissia, p. 25	Lunularia, p. 24	Conocephalum, p. 23	Cryptomitrium, p. 15	Asterella, p. 18	Reboulia, p. 14	Clevea, p. 13	Targionia, p. 12
Stalked receptacles present.....		+	+	+	+	+	+	+	+	+
Dorsal epidermis with trigones which distinctly bulge into the cells.....		+	+	+	+	+	+	+	+	+
Epidermal pores of thallus simple or barrelshaped.....		b	b	s	s	s	s	s	s	s
Antheridia on stalked receptacles.....		+	+	+	+	+	+	+	+	+
Thallus branching dichotomously.....		+	-	+	+	+	+	+	+	±
Number of rings of quite different cells by which pores are surrounded in surface view.....		1	2-3	4	4-5	2-3	1-3	3-4	1	2-3
Gemmae cups round, crescentic, none.....		r-n	n	c	n	n	n	n	n	n
Stalk of female receptacle with 0, 1, 2 furrows.....		2	2	0	1	1	1	1	0	
Wall of capsule with semiannular thickenings.....		++	++	-	++	-	-	-	+	+
Air chambers containing photosynthetic filaments.....		s	h	r	c	d	c-h	c-h	d	
Female receptacle cruciate, conic, hemispheric, stellate, diskshaped.....		+	+	-	-	±	+	-	-	-
Pseudoperianth present.....		+	+	-	-	-	±	+	-	-
Dorsal air chambers divided by supplementary partitions.....		-	-	-	-	-	±	+	-	-
Diameter of spores in mu.....		12-15	50-60	14-17	70-90	30-50	48-135	65-76	44-60	65-75
Ventral surface of thallus black-purple, purple, reddish-brown, green.....		r	r	r	g	g-p	p	p	g-p	b
Ventral scales of the thallus purple or hyaline.....		p-h	p	h	p-h	p	p-h	p	h	p

- GG. Gemmae cups crescentic; walls of capsule without semiannular thickenings; spores 14-17 μ ; female receptacle cruciate, its stalk without furrow.

Lunularia, p. 24

- BB. Epidermal pores of the thallus barrel-shaped; antheridia on stalked receptacles.

- H. Female receptacle hemispheric; spores 50-60 μ ; thallus not dichotomously branched; gemmae cups none.

Preissia, p. 25

- HH. Female receptacle stellate; 12-15 μ ; thallus dichotomously branched; gemmae cups sometimes present, round.

Marchantia, p. 26

TARGIONIA

Thallus light green above, thick coriaceous, with purple margins, forming thick mats or with other bryophytes, simply 1-3 times dichotomous or with adventitious innovations which ultimately become detached, broadly costate, gradually reduced to a unistratose margin; areolae indistinct; pores simple, prominent; air chambers in a single layer with chlorophyll in branch-like filaments within them; epidermal cells thick; trigones present; ventral scales present, in two rows, purple, triangular; appendages linear, unistratose except at base, occasionally hyaline cells present; rhizoids numerous, long, tuberculate or smooth; gemmae none; archegonia in groups, arising back of apex, becoming ventral by overarching, only a single archegonium developing in an involucre; involucre laterally compressed, obovoid or subglobose, 2-valved; valves united to form a suture, rigid, entire, brown or purple or black; pseudoperianth none; capsule dehiscing irregularly; walls unistratose, with spiral or semiannular thickenings; spores spherical, opaque; outer surface in ridges or wart-like folds; inner coat firm and its entire surface minutely and irregularly reticulate or granulate; elaters 2-4-branched, with 2-3 spiral bands, acute at ends; androecium small, lateral; branches disklike. We have only the following species:

1. *Targionia hypophylla* Linne.

Thallus green above, reddish brown or purple beneath; simple or sometimes dichotomous; obovate to sublinear; 5-20 mm long, 2-6 mm wide; apex rounded or slightly emarginate; costa 20-25 layers thick,

suddenly reduced to unistratose margin; margins involute, erect-connivent on drying; scales closely imbricate, superior one extending to margin; scale-appendages subentire, linear, contorted, dentate or ciliate; monoicous; spores brown, .05-.08 mm in diameter; elaters .15-.33 mm long, .006-.012 mm wide.

On shady banks, mostly on rocky soil. Cathlamet (Foster), Feb. 1907; Mount Rainier (Foster), 1909.

Oregon: Portland (31).

CLEVEA

Thallus simple or once dichotomous, sometimes innovating from near the apex, distinctly areolate; areolae slightly elevated; pores bounded by cells with radially thickened walls; air chambers numerous; their walls unistratose, in several series, occupying all of the margin and most of the median thickness; scales conspicuous, hyaline, sometimes tinged with purple, rarely purple thruout, obtuse or acute or acuminate, sometimes exceeding the margins; dioicous; archegonial branch dorsal, arising at median line some distance from apex, simple or in 1-4 series; its stalk pellucid, without rhizoid-furrows; receptacles more or less simple, 4-lobed; lobes obovoid, down curving, laterally compressed, bilabiate to middle, usually directly attached to stalk; pseudoperianth none; capsule nearly sessile, more or less included, dehiscing to middle or below by 3-8 irregular valves, walls of its cells with numerous annular or spiral thickenings; spores yellowish to brownish red, densely papillate; papillae large, obtuse; elaters with 2-4 spirals; antheridia immersed, scattered along the median line. We have only the following species.

1. **Clevea hyalina** (Sommerfelt) Lindberg. Not. Sällsk. pro Fauna et Fl. Fennica 9:291. 1868.

Marchantia cruciata Sommerfelt, Suppl. Fl. Lapp. p. 79, 1826. Not *M. cruciata* L. 1753.

Marchantia hyalina Sommerfelt, Mag. Naturvid. II. 1:284. 1833.

Sauteria alpina Angstroem, Bot. Notizer 1839:97 in part. 1839. Not *S. alpina* Nees, 1838.

Grimaldia punicea Wallroth, Linnæa 14:687. 1840.

Sauteria seriata Lindberg, Hedwigia 5:33. 1866.

Sauteria (Clevea) hyalina Lindberg, Oefv. Sv. Vet.—Akad. Foerh 3:561. 1866.

Sauteria succica Lindberg, Gottsche & Rabenhorst Hep. Eur. Exsic. No 347. 1866.

Plagiochasma erythrospermum Sullivant, Aust. Proc. Acad. Phila. 1869:229. 1870.

Sauteria limbata Austin, Proc. Acad. Phila. 1869:229 in part. 1870.

Clevea hyalina suecica Lindberg, Bot. Notiser 1877:78. 1877.

Clevea suecica Lindberg, Musc. Scand. p. 1, 1879.

Aytonia erythrosperma Underwood, Bull. Ill. Lab. Nat. Hist. 2:43. 1884.

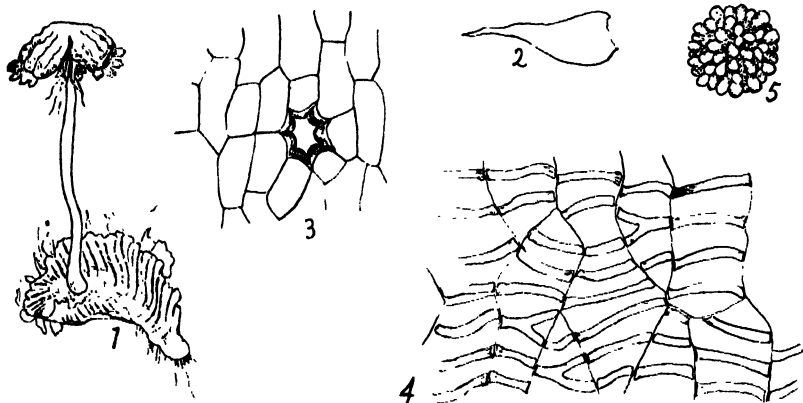
Clevis hyalina californica M. A. Howe, Mem. Torr. Bot. Club 7:38. 1899.

Thallus more or less strongly concave or canaliculate above, green or brown, sometimes with a hyaline border, narrowly oblong to obovate; simple or dichotomous, rarely innovating from apex, 5-12 mm long, 2-6 mm in greatest width; costa very prominent, of many layers, becoming thinner at margin; margin unistratose; scales numerous, purple at base but otherwise hyaline, or purple thruout, acute or acuminate, extending to margin of thallus; appendages with crenulate margins; dioicous; archegonial receptacles 2-5 mm broad, purple or reddish, underside with scales; capsule dehiscing irregularly by 3-6 valves; walls with semiannular thickenings; spores .045-.066 mm, reddish brown or very rarely yellowish; elaters brown, with 2-3 or rarely 4 spirals, .15-.3 mm long, .006-.015 mm wide.

On rocks in mountainous places. Alamota (Piper), April 1894; Elwha River Valley in Olympic Mts. (Frye), 1907.

Idaho (15).

Oregon (15).



Clevea hyalina. 1. Plant with female receptacle, $\times 2.5$. 2. Marginal scale of thallus, $\times 10.5$. 3. Surface view of pore, $\times 120$. 4. Thickenings in wall of capsule, $\times 340$. 5. Spores, $\times 225$. (1, 3, 5, after Janzen; 2, after Meylan; 4, after K. Mueller).

REBOULIA

Thallus dichotomously branched and innovating at the apex, coriaceous, without distinct areolae on the dorsal surface and with scattered simple pores, the originally simple air chambers becoming divided by secondary walls, rendering their limits indistinct; peduncle of female receptacle arising from behind the apex of a thallus-lobe, surrounded at base and apex by narrow scales, with a single rhizoid

furrow; receptacle conical or hemispherical, divided to the middle into 4-7 obtuse lobes, with air spaces and compound pores; involucre arising from the ventral margin of the receptacle-lobes, conchoidal and 2-valved, each enclosing a single sporogonium which does not fill the cavity; pseudoperianth absent; gemmae none; capsule subglobose, shortly pedicellate, with a large foot, irregularly dehiscing at the apex, the lower portion being left behind as a hemispherical cup containing the spores and elaters; elaters 2-3-spiral; male receptacle sessile, arising from behind the apex of a thallus-lobe, oval to semicircular, surrounded with small paleae. (Adapted from MacVicar).

1. **Reboulia hemisphaerica** (Linne) Raddi.

Thalli consisting of small rosettes or slightly extended layers, light green with usually a purple margin, 10-30 mm long and 6-8 mm broad, oblong or obcordate with emarginate or bilobed apex; margins ascending, crenulate; dorsal epidermal cells 4-6-angled with walls slightly and angles much thickened; pores little elevated, with 5-6 concentric rings, each of 6-8 cells having thickened angles; ventral surface purple; scales imbricate, in one row on each side of the midrib, obliquely lunate, with two linear acute appendages; chlorophyll-bearing layer strongly developed, occupying about half the midrib and almost the whole of the lamina; midrib thick, gradually passing into the lamina ending in a 1-celled margin; monoicous or dioicous; peduncle of female inflorescence 15-25 mm long; capsule-wall of a single layer of cells, without annular thickenings; spores 65-76 μ in diameter, rounded-tetrahedral, with a few large areolae and broad crenulate margin, brownish-yellow; elaters 300-450 μ long, 10-12 μ in maximum width, the apices subobtuse. (Adapted from MacVicar).

On soil along rivulet. At about 5000 feet altitude on Mt. Angeles near Port Angeles (Frye), 1927.

It has been reported by Howe from California (38), by Evans from Colorado (16) and by Macoun from British Columbia (41). Its occurrence in all of the states of our area would not be surprising.

CRYPTOMITRIUM

Thallus green above, green and purplish beneath, thin, 6-15 mm long, 3-10 mm wide, simple or 1-2 times dichotomous, sometimes with an apical and lateral innovations arising from the costa; branches obovate or ovate or oblong; areolae more or less veined; pores simple, walls of pores of oblong surrounding cells whose walls are un-

thickened; air chambers in 3-5 layers in median parts, of one layer in wings, separated by unistratose lamellae; margins brown or purple or green, undulating or crenate, slightly ascending, with an unistratose border 1-3 cells wide; costa prominent, 15-20 cells thick, gradually thinning to unistratose margin; moniocous; archegonial branch arising from apex of costa; stalk slender, naked, pale or brown, grooved, its posterior side without assimilating tissue, its ventral surface with hair furrow; receptacle more or less circular, flattish, convex, papillate above, naked and flat below; its margin thin, crenate, with 3-8 hair-canals connecting with that of the stalk; canals reaching half way to margin; air chambers in one layer; pores doliform; archegonia in groups of 4, alternating with the hair-furrows; sporophytes usually 5; calyptra inconspicuous; capsule nearly spherical, its upper one-third or one-fourth bistratose and serving as an operculum, otherwise unistratose; cell walls thin, without annular or spiral thickenings, sometimes thickened at angles; spores brown, more or less tetrahedral, areolate-lamellate; margins pellucid; elaters contorted, attenuated, often branched, with 2-3 spirals. The only recognized species is the following.

1. **Cryptomitrium tenerum** (Hooker) Austin, by Underwood in Bull. Ill. State Lab. Nat. Hist. 2:36. 1884.

Marchantia tenera Hooker; Kunth, Syn. Pl. 1:45. 1822.

? *Dryalia gayana* Montague, Ann. Sci. Nat. III. 4:354. 1845.

Dryalia tenera Gottsche; G.L.N. Syn. Hep. p. 554, 1846.

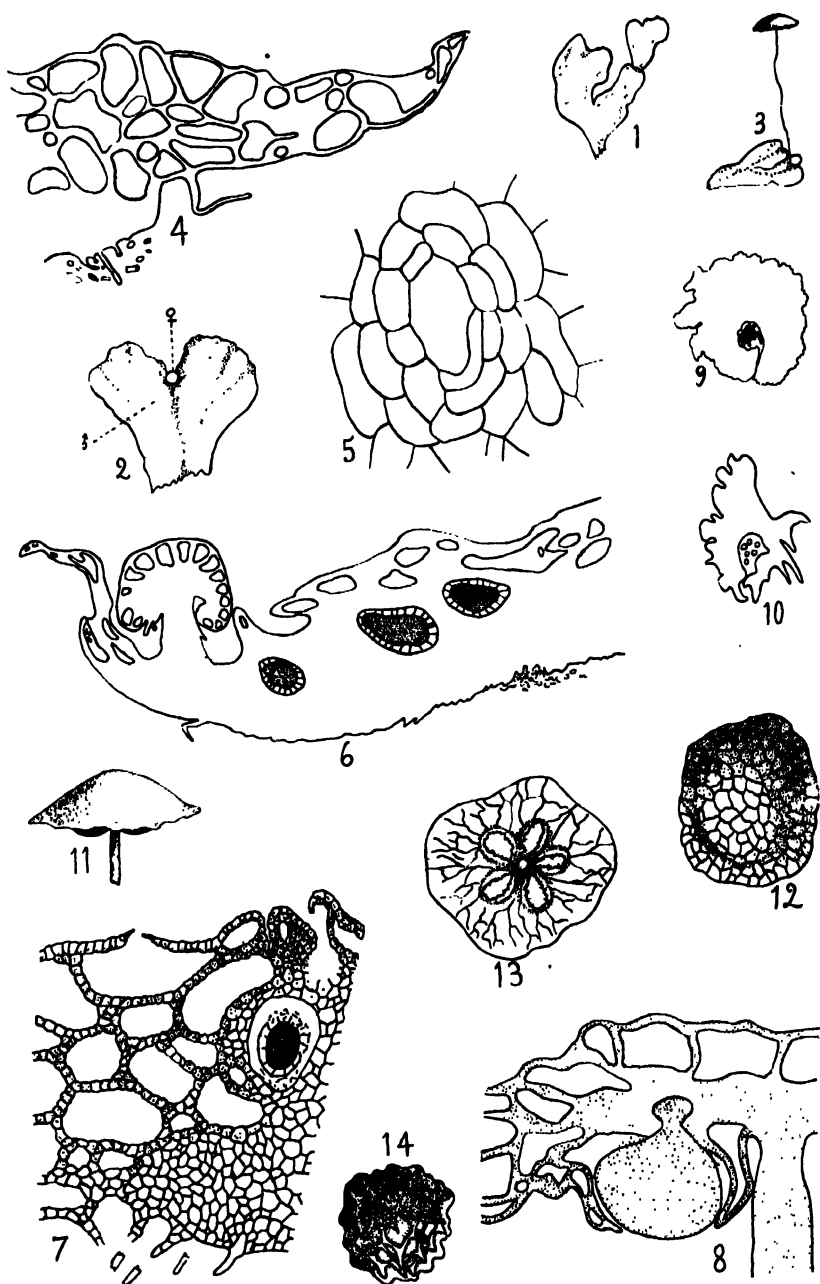
? *Dryalia brevipedunculata* Montague; G.L.N. Syn. Hep. p. 555, 1846.

Platycoaspis tenera Lindberg; Lindl. & Arnell, Sv. Vet.—Akad. Handl. 235:11. 1889.

Stalk of archegoniophore 1-3.5 mm long; spores .035-.05 mm; elaters .3-.45 mm long.

On moist banks. Elwha River Valley in Olympic Mts. (Frye), 1907; Snoqualmie Pass in Cascade Mountains (Frye), 1922.

Cryptomitrium tenerum. 1. Lobe of thallus with new extension, $\times 1$. 2. Lobe of thallus with young female receptacle, $\times 3$. 3. Lobe of thallus with mature female receptacle, $\times 1$. 4. Cross section of thallus from middle to margin, $\times 23$. 5. Surface view of pore, $\times 225$. 6. Longitudinal vertical section showing female receptacle and antheridia, $\times 23$. 7. Cross section near middle of thallus showing antheridium, chambers and pore, $\times 41$. 8. Semi-diagrammatic vertical section thru part of female receptacle showing mature sporophyte, $\times 23$. 9. Outline of cross section of stalk of young female receptacle, $\times 25$. 10. Outline of cross section of stalk of mature female receptacle, $\times 53$. 11. Female receptacle, $\times 4$. 12. Dorsal view of female receptacle, $\times 4$. 13. Ventral view of female receptacle, $\times 4$. 14. Surface of spore, $\times 310$. (After Howe).



CRYPTOMITRIUM TENERUM

ASTERELLA Beauvois (FIMBRIARIA Nees)

Thallus simple or sparingly dichotomous, sometimes innovating from in front or laterally from the costa, very thick in center, with thin margin, dark purple beneath; dorsal surface with distinct pores and areolae which become obscure in drying; air chambers deep or rather small and shallow, separated by plates of green cells; scales violet or rarely white; pores simple; cells about pores with unthickened walls; monoicous; archegonial receptacles usually obscurely lobed, conic or subhemispheric or flattened with age, its pores doliform; stalk with one rhizoid-furrow dorsally, assimilating tissue ventrally; involucre membranous; pseudoperianth at first conic, becoming exerted, 5-18-cleft, segments free or coherent; antheridial receptacles along costa or main thallus or on lateral branches, raised or obscurely defined; sporophytes 1-4 or rarely 6; capsule globose or oval or obovoid, usually dehiscing with an operculum, rarely the upper portion breaking apart; its walls usually thin, unistratose; its walls without thickenings or with evident trigones; seta short; foot bulbous; spores large, yellow or brown or black, obscurely tetrahedral or flattened; margin of spore pellucid, areolate-reticulate, verrucose, irregularly wrinkled; elaters with 1-4 spirals.

- A. Dorsal air chamber not divided by supplementary partitions; one pore to a chamber; dorsal epidermis of thallus with thin walls; segments of pseudoperianth free; archegonial receptacle distinctly lobed; spores yellow, 60-65 μ . 1. *A. ludwigii*
- AA. Dorsal air chamber more or less divided by supplementary partitions; several chambers to a pore; dorsal epidermis of thallus with thickened walls; spores 80-100 μ .
 - B. Margins of thallus not at all or scarcely incurved when dry; ventral scales purple; appendages of scales not forming a white cluster at apex; spores dark purple; plants not of a dry habitat. 2. *A. lindenbergiana*
 - BB. Margins of thallus strongly incurved when dry; ventral scales white; appendages of scales forming a white cluster at apex of thallus; spores yellow-brown; face of spores with ridges; plants of more or less dry habitat. 3. *A. saccata*

Comparison of species of <i>Asterella</i>	1. ludwigii	2. lindenbergiana	3. saccata
Cells of the dorsal epidermis with thickened walls.....	—	+	+
Dorsal air chambers divided by supplementary partitions.....	—	+	+
Pores per chamber 1 or more.....	1	m	m
Stalk of female receptacle with scales at base, or apex, or scarcely any.....	s	b+a	b
Segments of pseudoperianth free or connate at tips.....	f	c	c
Diameter of spores in mu.....	60-65	80-100	80-90
Trigones present.....	+	—	±
Ventral scales of thallus purple or hyaline....	p	p	h
Length of appendages of ventral scales in mm.....	.2-6	.25-.4	.7-1.
Pseudoperianth purple or white.....	w	p	w
Number of clefts in pseudoperianth.....	8	12-16	8
Elaters yellow, brown or purple.....	y	p	y-b
Spores yellow, brown or purple.....	y	p	y-b
Number of rings of modified cells about pore..	2	3-4	2-3

1. ***Asterella ludwigii*** (Schwaegrichen) Underwood, Bot. Gaz. 20:61. 1895.

Marchantia tenella Retzius, Fl. Scand. Prodr. ed. 2, p. 270, 1795. Not *M. tenella* L. 1753.

Marchantia pilosa Wahlenberg, Fl. Lapp. p. 399, 1812. Not *M. pilosa* Hornem. 1810.

Marchantia ludwigii Schwaegrichen, Hist. Musc. Hep. Prodr. p. 33, 1814.

Marchantia gracilis Weber, f. Hist. Musc. Hep. Prodr. p. 105, 1815.

Fimbriaria nana Lindenberg, Nova Acta Acad. Leop.-Carol. 12:Suppl. 109. 1829.

Marchantia nana Schleicher; Lindberg, Nova Acta Acad. Leop.-Carol. 14:Suppl. 110, as synonym. 1829.

Fimbriaria pilosa Taylor, Trans. Linn. Soc. 17:386. 1837.

Fimbriaria gracilis Lindberg, Not. Sällsk. Faun. Fl. Fenn. 10:282. 1868.

Asterella pilosa Trevisan, Rend. 1st. Lomb. II:7:785. 1874.

Fimbriaria ludwigii Limpricht; Cohn, Krypt. Fl. Schlesien 1:340. 1876.

Hypnantron gracile Trevisan, Mem. 1st. Lomb. 13:440. 1877.

Hypnantron nanum Trevisan, Mem. 1st. Lomb. 13:440. 1877.

Hypnantron pilosum Kuntze, Rev. Gen. p. 89, 1891.

Asterella gracilis Underwood, Bot. Gaz. 20:61. 1895.

Fimbriaria macounii Stephani, Bull. Herb. Boiss. 7:99. 1899.

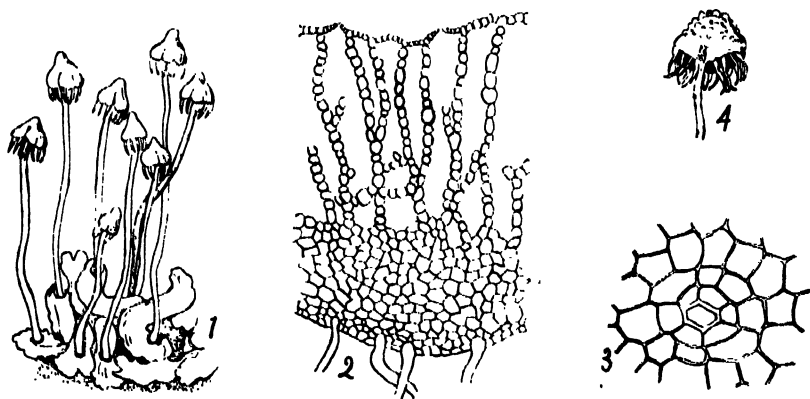
Thallus green or reddish brown, purple, simple or once dichotomous, oblong or ovate, 4-12 mm long, 1-3 mm wide, canaliculate or broadly concave, more or less distinctly areolate and porose, 25-35 cells thick at costa; margins purple, narrow, ascending, crenulate or undulate, on drying sometimes connivent; air chambers deep; scales

purple, reaching to the margin and beyond; rhizoids colorless, numerous, long; monoicous; archegonial receptacles arising from main thallus or principal branch, subglobose, 1-3 mm in diameter, nearly smooth, becoming wrinkled on drying; margins thin, obscurely lobed; lower surface naked; stalk 1-4 mm long, brown or red, smooth, surrounded at base by a few scales; pseudoperianth white, 5-12-cleft; its segments free, spreading or connivent; antheridia a little back of archegonial branch, few, immersed; capsule yellow, usually dehiscing about the middle; spores yellow or golden brown, .045-.06 mm in diameter; margins narrow, areolate-reticulate, sometimes with shallow alveolae; their meshes 5-12 across the face; their walls and angles thickened; elaters yellow or brown, with 2-4 spirals, attenuated at ends, sometimes branched.

On damp soil. Yakima region (Brandege), 1882; Mount Rainier (Piper), 1895; Cathlamet (Foster), 1907; Elwha River Valley in Olympic Mts. (Frye), 1907; Queets River Valley in Olympic Mts. (Frye), 1907; Tacoma (Flett), year (?); Silvercrest Falls (Foster), 1909; Cloudy Pass in Glacier Peak Region (Winona Bailey), 1910; Gate (Foster), 1912; Cascade Mountains (Frye), 1922.

Oregon: Portland (31); Silver Creek Falls in Marion County (Foster), 1910.

Montana: Long Baldy in Little Belt Mountains, Sperry Glacier, (20); Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928.



Asterella ludwigii. 1. Group of plants, $\times 2$. 2. Part of cross section of thallus, $\times 50$. 3. Surface view of pore, $\times 170$. 4. Female receptacle, $\times 2.5$. (1, after Bischoff; 2-4, after K. Mueller).

2. **Asterella lindenberghiana** (Corda) Lindberg, Musci Scand.

p. 1. 1879.

Fimbriaria lindenberghiana Corda; Nees, Naturg. Eur. Leberm. 4:283. 1838.

Fimbriaria bonjeanii DeNotaris, Mem. accad. Torino II. 1:335. 1839.

Asterella bonjeanii Trevisan, Rend. Ist. Lomb. 11:785. 1874.

Hypnantron bonjeanii Trevisan, Mem. Ist. Lomb. 13:440. 1877.

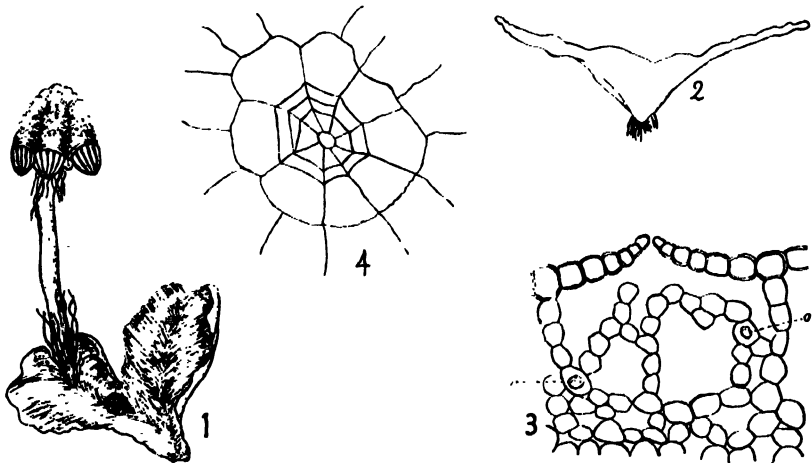
Hypnantron lindenberghianum Kuntze, Rev. Gen. p. 89, 1891.

Fimbriaria commutata Stephani Bull. Herb. Boiss. 7:202. 1899.

Thallus green, or reddish brown, prostrate, dichotomous, 1-3 cm long, 6-9 mm wide; branches linear; upper surface flat; pores visible and giving thallus a punctate appearance; chlorophyll layer 1/3 thickness of the thallus, extending to margins and thinner; air chambers large, becoming smaller at epidermis; margins undulate, thin, red; ventral surface red; scales violet-red, at margins numerous, round or triangular; appendages 1-2; lanceolate; rhizoids arising along keel. numerous, colorless; monoicous; archegonial branch a lateral innovation arising from the costa of the thallus, 6 mm broad, reddish brown; top rounded, somewhat papillose; margin 2-4-lobed; stalk 1-3.5 cm long, reddish brown, covered with scales or hairs; pseudoperianth large, violet-red, balloon-shaped, 16-lobed, coherent at apex; androecia slightly raised on papillate discs along middle of thallus; spores purple, opaque, .06-.09 mm in diameter, papillate; elaters with 1-3 spirals, short, narrow, violet-red.

On wet soil. Queets and Elwha River Valleys in Olympia Mts. at an altitude of 4500 feet (Frye), 1907; Mt. Angeles near Port Angeles (Frye), 1927.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.



Asterella lindenberghiana. 1. Plant with female receptacle, $\times 2.5$. 2. Diagrammatic cross section of thallus, $\times 75$. 3. Longitudinal vertical section thru pore; o, oil body, $\times 105$. 4. Surface view of pore, $\times 360$. (1-3, after K. Mueller; 4, after Meylan).

3. **Asterella saccata** (Wahlenberg) Evans, Contrib. U.S. Nat. Herb. 20:276. 1920.

Marchantia fragrans Schleicher, Pl. Crypt. Exsic. Hedvet. 3: No. 64, hyponym. 1804. Decandolle, Fl. Fr. 2:423. 1805. Not *M. fragrans* Balbis. 1804.

Marchantia saccata Wahlenberg, Ges. Nat. Freunde Berlin Mag. 5:296. 1811.

Fimbriaria saccata Nees, Horae Phys. Berol. p. 45, 1820.

Fimbriaria fragrans Nees, Horae Phys. Berol. p. 45, 1820.

Hypnantrum ciliatum Corda, in opiz, Beitr. p. 648, 1829.

Marchantia umbonata Wallroth, Linnaea 14:686. 1840.

Fimbriaria umbonata Wallroth, G. L. N. Syn. Hep. p. 559, 1846.

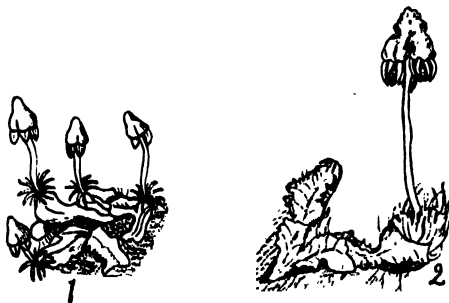
Asterella fragrans Trevisan, Rend. 1st. Lomb. II:7:785. 1874.

Hypnantron fragrans Trevisan, Mem. 1st. Lomb. 13:440. 1877.

Hypnantron umbonatum Trevisan, Mem. 1st. Lomb. 13:440. 1877.

Hypnantron saccatum Trevisan, Mem. 1st. Lomb. 13:440. 1877.

Thallus green above, purple underneath and at margins, 5-10 mm long, 2-3 mm wide, round or bluntly keeled, margin undulate, strongly incurved when dry, dichotomous; epidermal cells with walls somewhat thickened and often with distinct trigones; pores more or less elevated, surrounded by 6 radiating series of cells, two cells in a series; dorsal air chambers subdivided by supplementary partitions, chambers more numerous than pores; appendages of ventral scales 1-2, more or less connate, long acuminate, hyaline, forming a dense apical cluster; paroicus; archegonial branch with dense cluster of lanceolate hyaline scales at base, more or less pigmented; receptacle conical, 3-4-lobed, lobes extending downwards; involucre entire or sinuate; pseudoperianth white, 8-cleft, segments united at tips; operculum intact; spores brownish yellow, .08-.09 mm in diameter, wings wavy, surface covered with fine more or less regular reticulation, or smooth or with



Asterella saccata. 1. Group of plants, $\times 1$. 2. Plant, $\times 2$. (1, after Bischoff; 2, after Janzen).

folds or tubercles never forming a reticulum; elaters unispiral throughout or bi- or tri-spiral at middle.

Evans reports it from Colville (20).

Idaho: Kootenai County (Leiberg), 1891.

Montana: Swiftcurrent Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

CONOCEPHALUM

Thallus green or brown, large, dichotomous; dorsal surface distinctly areolate; areolae usually hexagonal; pores simple, large, forming elevations visible to the unaided eye; costa distinct, narrow, 20-35 cells thick, chlorophyll layer thin; cells of air chambers sometimes with conic or long-cylindric colorless beak; rhizoids long, numerous, arising in tufts along costa; scales purple, imbricate, apical ones with expansions at apex; marginal scales none; gemmae-cups none; archegonial receptacles obtusely conic, indistinctly or not at all lobed; long-stalked, when young a membranous sheath; stalk with 1 hair-furrow, without photosynthetic tissue; involucre 4-11, tubular, at maturity consisting mostly of the receptacle, each surrounding a single sporophyte; pseudoperianth wanting; capsule oblong-pyriform, on a thick stalk, dehiscing to about the middle by 4-8 valves; valves recurved, irregular; walls unistratose, with spiral and annular thickenings; spores large, multicellular at maturity, papillate; elaters rather short, thick, with 2-4 spirals; androecium terminal on an apparently lateral branch, disc-like, sunken in a depression bounded by somewhat scarious-membranous elevation of the dorsal layers of the thallus, strongly papillate. There is only the following species.

1. *Conocephalum conicum* (Linne) Dumortier.

In moist, deeply shaded places, especially on rocks and logs along streams. Olympia (Bell Page), 1883; Seattle (Piper), 1891; Olympia (Henderson), 1892; Tacoma (Flett), 1904; Deadman's Creek in Spokane County (Bonser), 1906; Queets River Valley in Olympic Mts. (Frye), 1907; Mount Rainier (Foster), 1909; Elliott (Clark), 1910; Yacolt (Frye), 1911; Burlington (Clark), 1911; Pacific Beach (Foster), 1911; Kalama (Frye), 1911; Heybrook (Clark), 1913; Chico (Frye), 1915; Eagle Gorge (Frye), 1923; Friday Harbor (Wentworth), 1823; north side of Orcas Island (Clark), 1925; Olga (Clark), 1925.

Oregon: Latourelle Falls (31); Silver Creek Falls (Foster), 1910; Cascadia (Van Wert), about 1922; Cape Arago (Frye), 1922.

Idaho: Moscow Mountain (Clark), 1924.

Wyoming: Lower Fire Hole Basin in Yellowstone National Park (42).

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

LUNULARIA

Thallus moderately large, dichotomous or progressing by innovations from apex, with effuse median thickening; lobes oblong, with a hyaline unistratose margin, 1-4 cells wide; areolae indistinct after drying; pores simple, visible to the unaided eye; cells surrounding pores elevated, often whitish and visible; chlorophyll-bearing layer shallow; occasional cells of colorless layer containing a large oil-body; gemmae-cups present, crescent-shaped; their margins thin, wanting in front; dioicous; archegonial receptacle arising from deep sinus of the thallus, in youth surrounded by a tubular-ovate sheath consisting of a number of scales; its inner scales membranous, hyaline, ciliate-fimbriate; archegonia in 4 groups of 3-4 each, only 1 of each group forming a sporophyte; receptacle without pores or rhizoids, consisting at maturity almost entirely of the slightly thickened top of the stalk and the 1-6 spreading tubular involucre surrounding each a single sporophyte; pseudoperianth wanting; stalk without rhizoid-furrow, delicate, pellucid, pilose, involucre at base; capsule dark brown, obovoid, rather long-stalked, exserted from bilabiate repand-mouthed involucre, dehiscing to base by 4 valves; valves often 2-parted, more or less twisted on drying; cell-walls without annular or spiral thickenings; spores yellow or brownish, smooth; elaters with 2 spirals, very long, slender, often adhering to end of valves for some time; androecium sessile, disc-like, papillate, surrounded by slight elevations of adjacent parts. The only recognized species is the following.

1. *Lunularia cruciata* (Linne) Dumortier.

In North America only the gemmiferous or sterile condition has been found except in the vicinity of San Diego, California. The crescentic gemmae-cups are always present on older plants and distinguish it from all our other liverworts.

In and about greenhouses. Kirkland (Jennie V. Getty), 1908; Seattle (Clark), 1927.

Oregon: Albany (Van Wert), about 1922.

Idaho: Moscow (Clark), 1926.

PREISSIA

Thallus green, often purple below, in thick mats, prostrate throughout, ventral shoots arising behind apical growing point; costa present, very prominent ventrally, many layers thick, gradually becoming thinner toward unistratose margin; border of margin 4-6 cells wide; dorsal surface more or less definitely areolate; pores one in center of each areolation, small, compound, surrounded by 4-5 superimposed rings of cells, lower pore-ring of 4 cells, upper pore-rings of 4-6 cells; cells of upper layer narrow, resinous grains present; lower cells large, projecting inward; air chambers in a single layer, filled with branched chlorophyll-bearing filaments; costa composed of compact cells, its upper layer 3-4 cells wide and containing chlorophyll, its other cells with oil drops and starch, older portions in cross section showing fibres with pointed ends and thickened walls; mycorrhiza present in compact layer, and fungus cells with thickened walls; ventral scales purple, in 2 rows, semi-orbicular, with triangular appendages; appendages with narrow base, fringed with projecting cells; rhizoids numerous, long, colorless; dioicous; subfloral innovation always present; archegonial receptacles terminal, long-stalked, bicanaliculate, 4-lobed; archegonia in 4 rows; upper surface of receptacle with pores; pores more convex than those of the thallus; lower surface with rhizoids and scales; sporophyte round, short-stalked; capsule projecting beyond the pseudoperianth, dehiscing by 6-7 valves, its wall unistratose except at base and apex; valves rolling backward; spores brown, granulate-papillate; elaters bispiral and brown, varying in length, rarely branched; antheridial receptacle a circular disc, stalked; ventral surface with scales; upper surface with small, conical prominences, each with a pore; antheridia in 3-6 rows; air chambers present. The only known species is the following.

1. **Preissia quadrata** (Scopoli) Nees.

On rocks or wet soil. Queets River Valley near foot of Humes Glacier in Olympic Mts. (Frye), 1907.

Montana: Iceberg Lake and Piegan Pass trails from Many Glaciers in Glacier National Park (Frye), 1928.

Wyoming: Lewis Lake in Yellowstone National Park (42).

MARCHANTIA

Thallus green or brownish, large, several times dichotomous; dorsal surface distinctly areolate; areolae rhombic; pores complex, doliform, usually more or less indistinct to the unaided eye; costa wide, effuse; air chamber layer strongly differentiated from the parenchyma layer, thick, filled with branched chlorophyll-bearing filaments; scales present; rhizoids numerous, long, colorless; gemmae-cups present, arising from the dorsal side of the costa, their margin dentate; archegonial receptacle stellate, rarely subentire, with 4-11 rays; rays finger-like, curved, spreading, each with 1 free or enclosed root-hair furrow; stalk long, with 2-3 rhizoid-furrows; archegonia in groups, number in groups various, alternating with the rays, one less than the number of the rays, each group enclosing at maturity several sporophytes; sporophytes enclosed by involucre; involucre bivalved, fimbriate, membranous; pseudoperianth cleft; capsule borne on rather short stalk, exerted beyond pseudoperianth, dehiscing by several valves or teeth; valve revolute; spores usually smooth; elaters long, narrow, with 1-4 spirals; androecium disc-like, long-stalked; margin thin, crenate, stellately or palmately lobed; ventral scales present. We have only the following species.

1. *Marchantia polymorpha* Linne.

Thallus green or brownish, prostrate, rarely ascending or sub-erect, forming wide mats, linear or oblong, 5-25 cm long, 2-10 cm wide, usually several times dichotomous; midrib wide, 16 cells thick, becoming thinned to unistratose margin; margins undulate crisped or lobed; areolae rhombic; pores more or less indistinct to unaided eye, composed of 4 concentric rings of 4 cells each; ventral surface brownish; rhizoids tuberculate and smooth, colorless or yellowish, numerous; scales colorless, tinged with brown or purple, 3 rows on each side of midrib; marginal scales ligulate, hyaline or purple; dioicous; archegonial receptacle stellate with 8-11, usually 9 finger-like projections; involucre fimbriate; segments ciliate-lanceolate or subulate or acuminate, brown; stalk of receptacle 2-8 cm long, more or less hairy; rhizoid furrows 1-3; posterior surface with pores and air chamber layer; capsule exerted, subglobular, stalked, 1-1.5 mm in diameter, dehiscing by 4-8 irregular valves; valves recurved; walls unistratose, with annular thickenings; spores yellow, .012-.015 mm, smooth; elaters attenuated, bistratose; gemmae rotund-reniform, disc-shaped, vertically inserted in groups at bottom of the goblet-shaped gemmae-cups.

On wet banks, in bogs, beside streams, very common. Easton, Lake Kechelus and Seattle (Röll), 1888; Seattle (Piper), 1891; Puyallup (Grace Colley), 1891; Tacoma (Horace Willeston), 1891; Lake Kechelus (Henderson), 1892; Spokane and Stevens Counties (F. O. Kreager), 1902; Crater of Mount Rainier (Frye), 1904; Biglow Gulch in Spokane County (Bonser), 1906; Queets River Valley in Olympic Mts. (Frye), 1907; Renton (Clark), 1910; Pacific Beach (Foster), 1911; Elwha River (Foster), 1911; Heybrook (Clark), 1913; Friday Harbor (Daugherty), 1923; Yakima (Van Wert), 1923; East Sound (Clark), 1925; Port Angeles (Frye), 1927. Common in the Puget Sound country.

Oregon: Mt. Hood (45); Rainier (31); Bridal Veil Falls (31); Mt. Hood (34, 38); Silver Creek (Foster), 1910; Albany (Van Wert), about 1920; La Grande (Frye), 1925.

Idaho: Moscow Mountain (Clark), 1923; Craig Mountain (Clark), 1924; Bovil (Clark), 1924; Pierce City (Gail), 1925; mouth of Salmon River (Lanney), 1927; Bonners Ferry (Frye), 1928.

Montana: Belton (40); Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928; Wolf Creek (Frye), 1928; Polson (Frye), 1928; Whitefish (Frye), 1928.

Wyoming: Head of Green River in Uinta County (42); Centennial Valley in Albany County (42); Mt. Washburn in Yellowstone National Park (Frye), 1925.

Order *Jungermanniales*

Gametophyte thalloid, simple or branched, not differentiated into distinct layers of tissue, with or without a costa, also transitional forms to gametophyte with cylindrical stem with leaves; chloroplasts several in a cell; the chlorophyllose region without air chambers; pores none; ventral surface with smooth rhizoids; sex organs in thalloid species in groups on the dorsal surface, but never on special stalked receptacles, and in leafy forms at end of special branches and in axils of leaves; first division of the embryo transverse, the lower of the two cells seldom taking any further part in the development of the sporophyte; sporophyte with a seta and a large foot; inner cells of capsule forming spores and in most species spirally thickened elaters; columella none; capsule in most species dehiscent by four valves.

- A. Capsule indehiscent; mature seta shorter than the capsule; each archegonium in a separate envelope; foot of the sporophyte much enlarged; elaters none. *Sphaerocarpaceae*, p. 28
- AA. Capsule dehiscent; mature seta longer than the capsule; several archegonia in one envelope; foot of the sporophyte not greatly enlarged; elaters present but sometimes rudimentary.
- B. Sex organs not at tip of stem or branch or costa; involucre not of leaves; plants thalloid except a few genera. *Metzgeriaceae*, p. 30
- BB. Sex organs at tip of stem or branch or costa; involucre composed of leaves; plants leafy. *Jungermanniaceae*, p. 46

Comparison of the families of Jungermanniales	Sphaero- carpaceae p. 28	Metzgeri- aceae p. 30	Junger- manniaceae p. 46
Elaters none, spiral or rudimentary.....	n	sr	sr
Archegonia each in a separate involucre.....	+	—	—
Antheridia each in a separate envelope.....	+	—	—
Involucre composed of leaves.....	—	—	+
Sex organs at tip of stem, branch or costa.....	—	—	+
Gametophyte leafy.....	—	±	+
Elaters bearers present.....	—	±	—
Thickness of capsule wall in cells.....	1	1-6	2-?

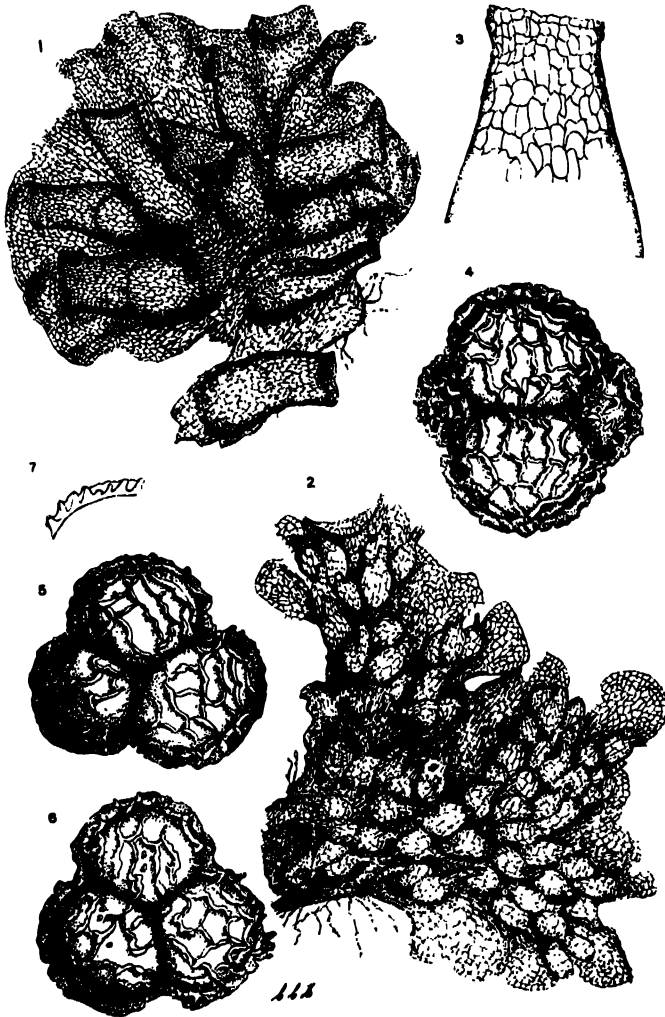
Family SPHAEROCARPACEAE

Gametophyte simple, thalloid, notched at margins, each notch a growing point with an apical cell; or else thallus somewhat elongated and the lobes constituting succubous leaves; dioicous; antheridia and archegonia scattered or somewhat aggregated, dorsal; antheridia spherical, each in a flaskshaped involucre; archegonia each in a subglobose or tubular involucre; calyptra ruptured; sporophyte with a bulbous foot, a short seta and a capsule; capsule of a single layer of cells, without special thickenings in the wall cells; elaters none. We have only the following genus.

SPHAEROCARPUS

Gametophyte thalloid, annual, small, orbicular to oblong, simple or forked, without midrib, several cells thick at center and gradually becoming thinner at margins; margins unistratose, 1 to many times

lobed; lobes reflexed or inflexed; cells thin-walled, quadrate to oblong pentagonal; trigones wanting; rhizoids colorless, smooth, thin-walled, numerous; dioicous; archegonia and antheridia on dorsal surface of thallus; archegonial involucre tubular, clavate, subglobose, sessile; calyptra ruptured early, a portion with the shriveled archegonium neck persisting long at apex of the capsule; capsule globose, with stalk and bulbous foot, indehiscent; walls of a single layer of cells, with or



Sphaerocarpus hians. Female plant, $\times 14$. 2. Male plant, $\times 29$. 3. Mouth of involucre, $\times 48$. 4-6. Tetrads of spores, $\times 390$. 7. Ridges of spores in optical section, $\times 390$. (After Haynes).

without annular or other thickenings; spores typical. We have only the following species.

1. **Sphaerocarpus hians** Haynes, Bull. Torr. Bot. Club, 37: 225. 1910.

Archegonial thallus oblong or orbicular, 4-6 mm in diameter, growing in isolated groups, bright green when dried; margins lobed and crispate, ascending; marginal cells usually quadrate; archegonial involucre 1-2 mm long, sessile, not crowded together nor covering the thallus entirely, tubular-ovoid, sometimes slightly larger at apex and flaring; mouth large, irregular, entire; cells of mouth with thick walls; antheridial thallus orbicular, 2 mm in diameter, forking several times, the leaf-like lobes curved over the involucre; involucre .243-.398 mm long, green but becoming brown and purplish with age; neck-cells thin-walled and nonprotuberant; capsule .587 mm long, the bulbous foot remaining attached to it; spores .066-.083 mm in diameter; golden brown, crispate-reticulate; crest of spore forming closed or partially closed meshes, or running in parallel lines towards the boundaries of the spores, a blunt spine sometimes in the areolae; spores permanently in tetrads.

In clayey places on bare alluvial soil in shade of willows at Pullman (Piper), 1894.

Idaho: Moscow (Clark), 1924.

This species was first placed under *Sphaerocarpus cristatus*. Haynes (Bull. Torr. Bot. Club, vol. 37, 1910) says "This species resembles most closely *Sphaerocarpus cristatus*, differing markedly in the involucre being tubular with a wide flaring orifice, instead of being subglobose with a small orifice, and in the tetrads remaining permanently united, while in *S. cristatus* they separate long before maturity. The spores of the two species are somewhat similar, though those of *S. hians* show more regular reticulations."

Family **METZGERIACEAE** (Jungermanniaceae Anacrogynae)*

Cells just behind the apical cell of the gametophyte transformed into archegonia; sporophyte arising dorsally or apparently from apex;

*We are using Underwood's (Bot. Gaz. 19:361. 1894) family name Metzgeriaceae in a restricted sense, including under it only those anacrogenous Jungermanniales which form claters. This leaves the family name Jungermanniaceae to include only the acrogynous Jungermanniales. We believe with certain authors that the order Jungermanniales is too large and too diverse in its extremes to be included within one family. We do not believe with those authors who split the order into many small families. Few and large families are of no disadvantage to the specialist, show relationships just as well, and are less confusing to beginners whose encouragement is highly desirable. The terms Jungermanniaceae anacrogynae and Jungermanniaceae acrogynae are too long and unwieldy as designations for groups.

leaf-organs generally lacking, in a few genera rudimentary; gametophyte thalloid to leafy, since all transitional forms approaching the leafy go here.

- A. Thallus with hairs on margins and midribs. *Metzgeria*, p. 36
- AA. Thallus without hairs on margins and midribs.
- B. Gametophyte leafy; leaves succubous. *Fossombronia*, p. 44
- BB. Gametophyte thalloid, simple; or if lobed the lobes not differentiated into distinct leaves.
- C. Margin of thallus regularly lobed with equal lobes; ventral surface with ovate toothed scales; gemmae of 2 kinds. *Blasia*, p. 43
- CC. Margin of thallus more or less simple or irregularly lobed; without ovate toothed scales; gemmae when present of 1 kind.
- D. Thallus 15-30 cells thick in middle; elaters 2-spiral; spores 33-49 μ , unicellular. *Moerckia*, p. 38
- DD. Thallus 10-16 cells thick in middle; elaters 2-4 spiral; spores 56-100 μ , multicellular. *Pellia*, p. 40
- DDI. Thallus 3-12 cells thick in middle; elaters 1-spiral; spores 10-24 μ , unicellular. *Riccardia*, p. 32

Comparison of genera of Metzgeriaceae	<i>Riccardia</i> , p. 32	<i>Pellia</i> , p. 40	<i>Moerckia</i> , p. 38	<i>Blasia</i> , p. 43	<i>Metzgeria</i> , p. 36	<i>Fossombronia</i> , p. 44
Gametophyte thalloid or leafy....	t	t	t	t	t	l
Gametophyte with hairs on margin or midrib.....	-	-	-	-	+	-
Underleaves none, or on young parts as toothed scales, or as hairs composed of single row of cells.....	n	n	h	s	n	n
Thickness in cells of thallus in its transverse middle region.....	3-12	10-16	15-30	5-10	5-8	
Diameter of spores in μ	10-24	56-100	33-49	33-43	21-42	40
Number of spirals in elaters.....	1	2-4	2	2	1	1-4
Thickness of capsule wall in cells.	2	2-?	3-6	3-4	2	
Inner wall of capsule with semi-annular thickenings.....	\pm	\pm	-	-	+	+

A. 'Thallus 3-8 mm wide, oily-lustrous; costa well differentiated.

1. *R. pinguis*

AA. 'Thallus not more than 2 mm wide, not oily-lustrous.

B. 'Thallus pinnate or bipinnate.

C. Unistratose margin 2-3 cells wide; cross section of thallus biconvex, 4-6 cells thick.

2. *R. multifida*

CC. Unistratose margin 1 cell wide or none, obsolete in older portions; cross section of thallus flat, 6-9 cells thick; margins sinuate.

3. *R. sinuata*

BB. 'Thallus palmately or irregularly branched.

D. Monoicous; cross section of thallus plano-convex, 5-6 cells thick in the middle; thallus branches frequently broadened toward the end.

4. *R. latifrons*

DD. Dioicous; cross section of thallus biconvex, 6-9 cells thick in the middle; thallus branches narrowed toward the end.

5. *R. palmata*

Comparison of species of Riccardia	1. <i>pinguis</i>	2. <i>multifida</i>	3. <i>sinuata</i>	5. <i>palmata</i>	4. <i>latifrons</i>
Width of thallus in mm.....	3-8	.35-.5	.5-1.5	.2-.35	.84-1.5
Thallus with an oily lustre.....	+	-	-	-	-
Depth of thallus in thickest part as measured in cells.....	10-12	6-7	6-9	6-9	5-6
Width of unistratose margin of thallus as measured in cells.....	2	2-3	0	0	1
Outer wall of capsule with nodular or semiannular thickenings.....	n	a	a	a	n
Branch tips of thallus tending to become wider or narrower or neither.....	e	a	e	a	w
Inner wall of capsule smooth, somewhat nodular or with semiannular thickenings.....	a	s	a	n	a
Thallus monoicous or dioicous.....	d	m	m	d	m

RICCARDIA (Aneura)

Plants thalloid, pinnately or palmately or subdichotomously branched, rarely subsimple, somewhat fleshy, composed of several layers of cells, outer cells small, inner cells elongated and larger; costa and wing either undifferentiated or plant with a unistratose margin (wing); wings 1-3 cells wide or sometimes quite wide and then costa present; rhizoids few; monoicous or dioicous or rarely

paroicus; archegonia several on short lateral branches, but appearing ventral by growth of thallus, confluent with thallus; margin of archegonial branch with narrow laciniae, sometimes produced by single cells; calyptra formed by thallus, pyriform or tubular, large, fleshy; its wall of many layers, rough with papillae or short trichomes especially when young; involucre inconspicuous; antheridia spherical, immersed singly in loculi, arranged in 2 parallel rows on short oblong branches; sporophytes long-stalked, oval or oblong-ellipsoid; capsule before opening with a short internal central column at apex, probably composed of 2 layers of the capsule wall; column or elater-bearer at dehiscence 4-parted, one part united to each valve at apex; elaters with 1 or rarely 2 spirals, more or less attenuated at ends, some clinging to elater-bearers and forming pencil-like tufts at valve tips; inner layers of capsule wall with annular or spiral thickenings; spores small; gemmae oval, 2-celled, endogenous.

1. **Riccardia pinguis** (Linne) S. F. Gray.

Thallus green or yellowish green, with a fatty lustre, prostrate or ascending, rigid on drying, 1-6 cm long, 3-8 mm wide, subpinnate or pinnate; costa definite, 8-12 layers thick; surface cells small, containing chlorophyll; inner cells hyaline, large; wing wide, mostly bi-stratose, border 2 rows wide; ventral surface and costa with colorless or yellow rhizoids; dioicous; antheridial and archegonial plants often intermingled, sometimes in separate mats; archegonial branch lacinate; archegonia 3-5; calyptra at maturity 10 mm long, tuberculate or smooth; sporophyte borne on long seta, round or oval; elater-bearers conspicuous; elaters contorted, yellow, thin, long, .145-.3 mm long, .009-.012 mm wide, of one broad band or two narrow spiral bands; spores brown, minutely papillate, .018-.024 mm; antheridial plants suborbicular to short oblong, geminate; margins entire or crenulate; antheridia 4-13, irregularly placed along costa.

On swampy ground. Ravenna Park in Seattle (Frye), 1904; Bowl and Pitcher along Spokane River in Spokane County (Bonser), 1907; South Bend (Frye), 1908; University Campus in Seattle (Rigg), 1910.

2. **Riccardia multifida** (Linne) S. F. Gray.

Thallus brownish-green to black on drying, prostrate, 2-3-pinnate, often forming radiating clusters of half-rosettes, 2-5 cm long; branches crowded, narrow, .35-.5 mm wide, biconvex with unistratose

border 2-3 cells wide; costa somewhat obscure, 4-6 cells thick; its cells .06-.102 mm long, .018-.036 mm wide, irregularly elongated; cells of wings hexagonal, .024-.36 mm in diameter, marginal cells smaller; monoicous or rarely paroicous; archegonial branch lateral, short; its margin copiously laciniate; laciniae generally 1 cell wide at apex; calyptra fleshy, very rough, 3-4 mm long; capsule dark brown, cylindric, 1.5-3 mm long, .5-.75 mm wide; spores light brown, .012-.015 mm in diameter; elaters attenuated, .25-.48 mm long, .015-.018 mm wide; antheridial branch distant from archegonial one or at its base, linear, oblong or oval; margin crenulate; loculi 5-6 pairs.

The sporophytes were either too young or too fragmentary; their description is an adaption from Warnstorf's *Kryptogamen Flora der Mark Brandenburg*.

On decaying wood and moist banks. Seattle (Piper), 1892; Ashford (Allen), 1905; Easton (Bertha Kilgour), 1905; Seattle (Frye), 1908; Bellingham (A. P. Romine), 1908; Pacific Beach (Foster), 1911; North side of Orcas Island in San Juan County (Clark), 1923; Friday Harbor (Clark), 1925.

Idaho: Moscow Mountain (Clark), 1923.

3. *Riccardia sinuata* (Dickson) Trevisan, Schema nuov. class. Epat. p. 431. 1877.

Thallus green to nearly black, in more or less thick mats, 2-3 cm long, .5-1.5 mm wide, regularly or irregularly pinnate; thallus segments simple or again pinnate, opaque, their central region 4-6 layers thick; unistratose border none; margin sinuate by short branches; surface cells .045-.105 mm long, .03-.06 mm wide, hexagonal or irregularly elongated; monoicous; archegonial branch rather broad, clavate-cylindric, 2.15-3.5 mm long, .7-1.36 mm wide, more or less roughened; margin somewhat papillose; capsule oblong-ellipsoid, dark brown to nearly black, its walls of several layers; elaters brown, .27-.5 mm in diameter; antheridial branch short, oval.

On very damp soil or sometimes submerged. Seattle (Piper), 1891; Whatcom Falls in Whatcom County (Romine), 1907; Friday Harbor (Clark), 1923; North side of Orcas Island in San Juan County (Clark), 1923.

Oregon: Otter Rock (Daugherty), 1921; Albany (Van Wert), about 1923.

3a. Variety **major** (Nees), n. comb.

Aneura multifida major Nees, Naturgesch. Eur. Leberm. 3:450. 1838.

Riccardia major Lindberg, Musc. Scand. 5. 1879.

Aneura sinuata major (Nees) MacVicar, Student's Handbook of Brit. Hep. 2nd ed., London, 1926.

Thallus usually simple or sometimes loosely and irregularly pinnate; unistratose margin 0-1 cell in width, middle 3-5 cells thick; margin of female branch multilacinate; capsule dark-brown or black; elaters 280-500 μ long, 10-14 μ wide, reddish-brown; spores brown, minutely papillose, 14-21 μ .

Since this variety has been reported by Howe from California and by Evans from Alaska, it will probably be found in our area, although such has not yet been the case.

4. *Riccardia latifrons* Lindberg.

Thallus light green to dark, somewhat palmately lobed; becoming black on drying, translucent when moistened, in thick mats or mixed with mosses; ultimate branches linear or oblong, 2-4 mm long, .84-1.5 mm wide, strongly emarginate, more or less concave dorsally, concave or plane ventrally; clearly differentiated costa none; central region 4-6 cells thick; unistratose margin 1 cell wide; surface cells pellucid, hexagonal, pentagonal or irregularly elongated, .045-.12 mm long, .024-.051 mm wide; monoicous; archegonial branch with numerous 1-celled lacinae; calyptra pyriform-clavate, verrucose near apex, 2.5-3.5 mm long, .5-1 mm wide in upper part; capsule brown, oval, dehiscing by 4 valves; spores yellowish brown, minutely papillate, .01-.016 mm in greatest diameter; elaters brown, .115-.3 mm long, .01-.015 mm wide; antheridial branch narrowed at base, united to base of archegonial branch; margin erect, lacinate; loculi 5 pairs.

In damp woods on decaying wood or logs. Seattle (Piper), 1891 and 1892; Cascade Mountains (Allen), 1903; Hamilton (Foster), 1905; Cathlamet (Foster), 1906; Olympic Mountains (Frye), 1907; Westport (Foster), 1908; Ilwaco (Frye), 1908; Burlington (Clark), 1911; Pacific Beach (Foster), 1911; Copalis (Foster), 1911; Yacolt (Frye), 1911; Hoodport (Foster), 1912; Friday Harbor (Daugherty), 1923; North side of Orcas Island in San Juan County (Clark), 1923; Trout Lake on San Juan Island (Clark), 1923; La Push (Frye), 1927.

Oregon: Portland (44).

Idaho: Moscow Mountain (Clark), 1923.

Montana: Polson (Frye), 1928.

Wyoming: Norris Geyser Basin in Yellowstone National Park (Frye), 1925.

5. *Riccardia palmata* (Hedwig) Carruthers.

Thallus dark green with the older parts reddish-brown, 5-10 mm long, .2-.35 mm wide; main stem closely attached to the substratum, with ascending or erect branches from its entire length; branches simple or furcate or palmate, linear, frequently narrowed at the round or truncate or emarginate apex, opaque when moist; cells of dorsal surface 5-6-angled, round, smaller than in *R. latifrons*, with thick walls which are reddish-brown except in the younger parts; cross section biconvex, 6-9 cells thick in the middle, the margins not unistratose; interior cells distinctly larger than the surface cells; dioicous; archegonal branches with a few short laciniae; calyptra to 2 mm long, cylindrical, strongly papillose; capsule wall with semiannular thickenings in outer layer, without semiannular thickenings but with slight nodules on the inner layer; spores .012-.015 mm in diameter, brown, almost smooth; antheridial branches, round or oblong or linear; margin incurved, crenulate; gemmae round or oblong, at apex of branches. (Adapted from MacVicar).

Evans (14) reports it from Washington.

Oregon: Silverton (Foster), 1910.

Idaho: Moscow Mountain (Clark), 1924.

METZGERIA

Thallus with linear lanceolate lobes, usually dichotomous, sometimes once branched, rarely with ventral branches arising along midrib; very rarely a cell at the margin developing into a gemma-like branch; gemmae shield-shaped; costa present, nearly round, narrow, its cells elongated, only the surface cells containing chlorophyll; wing wide, its cells hexagonal; ventral surface of costa and wing more or less hairy, rarely both surfaces hairy thruout; hairs rarely developed

Comparison of species of Metzgeria	1. conjugata	2. fruticulosa	3. pubescens
Upper surface of thallus hairy.....	—	—	+
Width in cells of costa dorsally.....	2	2	7-8
Width in cells of costa ventrally.....	4	4	7-8
Monoicous or dioicous.....	m	m	d
Gemmae none, or when present either on special upright branches, or just on surface of thallus.....	s	u	n
Marginal hairs of thallus solitary or in pairs...	p	s	s

into rhizoids; sex organs on much reduced ventral branches; archeogonial branch developing in upper part into a heart-shaped hemispherical hollow hipid tube without costa; antheridial branch suborbicular, curved, generally smooth, with costa; antheridia not sunken, on a 1-celled stalk; calyptra fleshy, thick, round, hairy; capsule oval, dehiscing by 4 valves; valves rigid, bistratose; elaters with 1 spiral, permanent, attached in bunches at apex of valves.

A. Only lower surface of costa and wings with hairs.

B. Wings nearly always without hairs on the under side; gemmae never present.

1. *M. conjugata*

BB. Wings generally with hairs on the under side and with single hairs just within margins; gemmae sometimes present on upright branches.

2. *M. furcata fruticulosa*

AA. Upper and lower surfaces of costa and wings with hairs.

3. *M. pubescens*

1. *Metzgeria conjugata* Lindberg.

Thallus light green or yellowish, more or less dichotomous, prostrate with apex ascending, forming thick mats, lobes elongated, lanceolate or linear, 5-40 mm long, 2-4 mm wide, not hairy at apex; costa narrow, 2 cells wide dorsally, 4 cells wide ventrally, 5-7 cells thick, abruptly thinned to wide unistratose margin, hairy beneath; dorsal surface of wing smooth, without hairs or rarely with scattered hairs at convex margin; gemmae orbicular, 1-celled; hairs simple; cells of costa .05-.65 mm long, .27-.045 mm wide, the inner cells .009-.015 mm in diameter; cells of wing hexagonal, .021-.045 mm in diameter; thick-walled cells with trigones; monoicous; archeogonial branch arising ventrally from along costa, short; calyptra obconic, bilobed after breaking by capsule, 1-1.5 mm long, hispid; capsule more or less long-stalked; elaters filiform, attenuate, with 1 spiral; spores brown, .021-.024 mm in diameter; antheridial branch ventral, subrotund, bent.

In damp woods on tree trunks. Enumclaw (Röll), 1888; Seattle (Piper), 1891; Puyallup (Cooley), 1891; Cascade Mountains (Allen), 1900; Friday Harbor (Foster), 1904; Hamilton (Foster), 1905; Guemes Island (Frye), 1905; North Bend (Frye), 1906; Cathlamet (Foster), 1907; Westport (Foster), 1908; Wynooche (Foster), 1909; Brinnon (Foster), 1911; Gate (Foster), 1911; Renton (Foster), 1912; Port Angeles (Foster), 1914; Eagle Gorge (Frye), 1921; Friday Harbor (Clark), 1923; Trout Lake on San Juan Island (Clark), 1925; North side of Orcas Island in San Juan County (Clark), 1925.

2. **Metzgeria furcata fruticulosa** (Dickson) Lindberg,
Monog. Metz. p. 40. 1877.

Thallus small, yellow-green, but becoming blue-green when dried, much furcate; some branches prostrate or ascending with broad apex; convex; with few oblong gemmae from margin or midrib; other branches suberect, more elongated and narrow, strongly convex with discoid or oblong gemmae from the margin and from both surfaces near the apex; midrib narrow below and usually of a few cells, on the branches broadened and of many cells, sometimes occupying almost the entire thallus of the suberect parts; branches sometimes flat, ascending, frequently without a midrib, margins with discoid or oblong gemmae; hairs numerous on wings and midribs, also on margins and just within them, single, rarely bearing gemmae.

Dr. A. W. Evans reports this by Foster from Aberdeen (Bryologist 14:87. 1911).

Oregon (12, 33).

3. **Metzgeria pubescens** (Schrank) Raddi.

Thallus light green or yellow, prostrate or with apices ascending, linear, subdichotomous, 1-3 cm long, 1.5-2 mm wide, densely hairy thruout on ventral and dorsal surfaces; hairs simple, colorless; costa 7-8 cells wide on both surfaces; 5-7 cells thick, abruptly thinned to unistratose wing; cells of costa .03-.06 mm long, .024-.036 mm wide, hexagonal, thin-walled, their trigones wanting or indistinct; margins not curved; dioicous; archegonial branch cordate, hairy to apex; antheridial branch more or less hairy, bent; capsule and spores undeveloped so far as seen.

On tree trunks. Cascade Mountains (Allen), 1900; Ashford (Allen), 1908; Duwamish River (Foster), 1911; North side of Orcas Island in San Juan County (Clark), 1923; Friday Harbor (Clark), 1925; Joyce (Frye), 1927.

Montana: Avalanch Basin, Holzinger Basin, Lake McDonald (40); Polson (Frye), 1928.

MOERCKIA

Thallus medium in size, green or olive, prostrate or ascending at apex, simple, dichotomous or with ventral branches arising sometimes from rhizome-like base, biconvex, abruptly narrowed to a unistratose wing; costa narrow, sometimes reduced; surface cells of costa narrowly elongated; inner cells of costa of thick-walled cells; wing broad, plane or crispate; cells of wing hexagonal; sex organs on

dorsal surface of thallus; archegonia surrounded by more or less toothed scales; pseudoperianth long, cylindrical or ovate, appearing at maturity of sporophyte, its mouth more or less contracted, its margin toothed or ciliate; calyptra fleshy; capsule oblong-cylindric, dehiscing unequally by 4 valves; spores small, minutely papillate; elaters filiform, long, with 2 spirals; antheridial branches in 1 row on each side of costa, more or less surrounded by toothed scales; antheridia large, on 1-celled stalk.

A. Plants robust; rhizoids golden-yellow; archegonial scales blunt; ridges on spores beset with short truncate spines.

1. *M. blyttii*

AA. Plants more delicate; rhizoids white or pale yellow; archegonial scales sharply cleft; ridges on spores smooth.

2. *M. flotowiana*

Comparison of species of <i>Moerckia</i>	1. <i>blyttii</i>	2. <i>flotowiana</i>
Rhizoids golden-yellow, white or pale yellow.....	g	wy
Diameter of thallus in mm.....	8-15	4-8
Maximum thickness of costa in cells.....	20-30	15-20
Involucre with broad lobes, or deeply lacinate.....	b	l
Diameter of spores in μ	30-42	42-49
Ridges of spores smooth or with short truncate spines.....	p	m

1. *Moerckia blyttii* (Moerck) Brockman.

Thallus pale green, caespitose, medium in size, 10-25 mm long, 8-15 mm wide, oblong, simple, prostrate, somewhat thick and submembranous; costa present, obscure on dorsal surface, prominent on ventral surface, 20-30 cells thick, abruptly or gradually thinned to unistratose margin; surface cells larger than inner, without trigones, with firm walls; inner cells small; wings curling over costa on drying; rhizoids golden brown, arising along costa; dioicous; archegonia dorsal, surrounded by bracts; bracts undulate-plicate, unequally lacinate; laciniae obtuse; pseudoperianth projecting beyond bracts, laterally compressed, fleshy, its upper part plicate, its mouth irregularly and unequally lacinate-dentate; capsule reddish-brown, 5-10 mm long, dehiscing by 4 valves; seta long; spores brown, .03-.04 mm in diameter, verruculose; verruculae beset with truncate spines; elaters light to dark brown, .15-.2 mm long, .007-.01 mm wide; antheridia dorsal, surrounded by 20-30 imbricate bracts; bracts 2-4-lobed; antheridia large, single, with a very thick style.

On wet rocks. Paradise Valley on Mount Rainier at 5000 feet (Flett), 1904; Near Humes Glacier in Queets River Valley in Olympic Mountains at about 5000 feet (Frye), 1907.

Evans (12) reported it from Ucluclet, British Columbia, in 1910. We know of no other North American localities.

2. *Moerckia flotowiana* (Nees) Schiffner.

Thallus green or yellowish, prostrate, simple or dichotomous, 10-30 mm long, 4-8 mm wide; costa 15-20 cells thick in center, strongly convex ventrally, slightly concave dorsally, usually with 2 strands of small lignified cells, abruptly thinned to unistratose wing; surface cells of thicker portion .9-1.4 mm long, .048-.054 mm wide, colorless; ventral cells of costa brownish; margin incurved, undulate and usually greatly crisped; rhizoids numerous, white or pale yellow, along the costa; dioicous; female involucre short, irregularly lacinate; pseudoperianth 5 mm long, 1 cell thick in upper part, 3-4 cells thick at base, cylindrical, frequently reddish-brown, mouth lobed and ciliate; calyptra shorter than the pseudoperianth, 1 cell thick above, 4-5 cells thick at base; capsule reddish-brown, cylindrical-oval, 3 mm long; seta 3 cm long; capsule wall of 5 layers of cells, its radial walls thickened and reddish, outer cells large, inner cells much smaller; spores reddish-brown, .042-.049 mm, ridged or reticulate; elaters reddish-brown, attenuate, bispiral; antheridia many, on the costa; bracts ovate, irregularly dentate. (Most of the description adapted from MacVicar).

On wet soil. Mt. Rainier (Flett), 1904; headwaters of Queets River (Frye), 1907; Friday Harbor (Clark), 1923.

PELLIA

Thallus growing in thick masses with closely imbricate ascending lobes or in nearly flat rosettes, bright green, becoming dark on drying, soft and flaccid, fleshy or thin, irregularly dichotomous; margin undulate to sinuate-lobed; ventral scales none; costa broad, indistinct, 9-16 cells thick, passing gradually into a unistratose wing; rhizoids numerous, brown, arising from the costa; archegonia 4-18 along dorsal side of costa in pockets near apex of thallus; involucre becoming dorsal, reduced to a scale at posterior side of cavity, tubular or a short narrow ring, its margin crenulate; calyptra exerted or included in the involucre, walls several cells thick; capsule round, long-stalked, light brown, dehiscing by 4 valves; walls bistratose; cells of inner layer with semiannular thickenings or rudimentary spirals; outer

layer with yellowish-brown trigones or nodulose thickenings; elater-bearers present, 20-200, persistent, attached to base of capsule, with 3-6 spirals, their free end thickened; elaters with 2-4 spirals, obtuse, together with the spores often remaining as a central mass; spores very large, at maturity multicellular, oval-ellipsoid, papillate; antheridia oval, short-stalked, emersed, single, arranged irregularly along dorsal surface of the costa.

Sterile forms of *Pellia* can not be told from each other with certainty and are often confused with *Riccardia pinguis*; the latter is distinguished by the pinnate branching, rounded apices, rigid texture and oily lustre.

A. Thallus in longitudinal section with vertical band-like thickenings; capsule wall with semiannular thickenings.

B. Margin of involucre absent on side towards apex of thallus; monoicous.

1. *P. epiphylla*

BB. Involucre a short tube; dioicous.

2. *P. neesiana*

AA. Thallus in longitudinal section without vertical band-like thickenings; capsule wall without semiannular thickenings.

3. *P. fabbroniana*

Comparison of species of <i>Pellia</i> and <i>Blasia</i>	PELLIA			BLASIA
	1. epi- phylla	3. fabbro- niana	2. nees- iana	pusilla p. 43
Under surface of gametophyte with ovate toothed scales (underleaves), or without scales.....	w	w	w	s
Rhizoids white or brown.....	b	b	b	w
Gametophyte with greasy lustre.....	+	+	+	—
Unistratose margin of gametophyte extending to costa, or a few (1-2) cells wide.....	f	f	f	c
Spores reticulate by depressions or smooth.....	s	s	s	d
Spores oval or round.....	o	o	o	r
Spores several celled, or apparently several-celled by depressions.....	s	s	s	d
Width of gametophyte branches in mm....	10-15	4-7	3-7	.5-5
Paroicous or dioicous.....	p	d	d	d
Involucre a short complete tube.....	—	+	+	+
Gametophyte with interlacing band-like thickenings in longitudinal section....	+	—	+	—
Inner wall of capsule with semiannular thickenings.....	+	—	+	—
Number of spirals in elaters.....	2	3-4	2	2
Diameter of spores in μ	80-100	56-77	80-100	33-43
Mouth of pseudoperianth incised, constricted-mammillate, crenate-lobed, ciliate-lobed, facinate-lobed.....	i	ci-l	cr	m
Length of mature seta in mm.....	20-50	10-20	20-50	20

1. *Pellia epiphylla* (Linne) Corda.

Thallus in flat compact mats, green or seldom red, 1-7 cm long, 10-15 mm wide, not collapsing when removed from water; costa convex ventrally, 14-16 cells thick, in longitudinal sections with vertical band-like thickenings; monoicous; archegonial involucre at apex of lobes along midrib, reduced to a scale on posterior margin of pocket-like cavity where calyptra arises; calyptra subcylindrical, 4-5 mm long, 4-5 cells thick, roughened by hairs; capsule brown or green, on long seta, dehiscing by 4 valves; inner cells with irregular semi-annular thickenings; outer cells with nodular thickenings; elater-bearers persistent, 10-30, contorted, short, stout, with 3-4 spirals; elaters very thin, with 2 spirals, intermingled with spores into a central mass; spores greenish, of several cells, thickly papillate, .075 mm wide, .1 mm long; antheridia immersed along costa.

In wet places. Seattle (Piper), 1891; Kalama (Frye), 1911.

2. *Pellia neesiana* (Gottsche) Limpricht.

Thallus green, reddish to black on drying, in thick mats or with mosses, prostrate, 7-15 mm long, 3-7 mm wide, not collapsing when out of water, simple or dichotomous; branches linear or oblong; costa flat or convex, 10-12 cells thick; wing unistratose, in longitudinal section the cells showing vertical colorless or reddish-brown thickenings; dioicous; archegonial involucre a short tube, 1-2 mm long; margin lacerate; calyptra exserted, 1-3 mm long; capsule spherical, 1.5 mm in diameter; seta long; inner cells of capsule with imperfect semiannular thickenings; contents of capsule in a tangled globular mass, more or less persisting after dehiscing of the capsule; elater-bearers stout, with 3-4 spirals, ends conical; elaters contorted, with 2 spirals, .225-.24 mm long, .009-.012 mm wide; spores 4-5 cells long, .084-.135 mm long, 2-3 cells wide, .051-.064 mm wide; antheridial plants in dense mats; margins crenulate and overlapping.

On wet rocks and soil along river banks. Ilwaco (Piper), 1904; Paradise Valley on Mount Rainier (Flett), 1904; Elwha River Valley in Olympic Mountains (Frye), 1907; Queets River Valley in Olympic Mountains (Frye), 1907; Ilwaco (Frye), 1908; South Bend (Frye), 1908; Tacoma (Flett) year (?); North side of Orcas Island in San Juan County (Clark), 1923; Friday Harbor (Wentworth), 1923; La Push (Frye), 1927.

Oregon: Cape Arago (Frye), 1922.

Idaho: Pierce City (Gail), 1924; Moscow Mountain (Clark), 1925.

3. *Pellia fabbroniana* Raddi.

Thallus in flat mats or in rosettes, often among mosses, 1-2.3 cm long, 4-8 mm wide, dichotomous, delicate, collapsing when taken out of the water; costa flat or convex, 14-16 cells thick; wing thin, in longitudinal section the cells without vertical reddish-brown or colorless band-like thickenings; dioicous; archegonial involucre upright, cylindrical, 4-5 mm long, its margin lobed; calyptra included, 3 mm long, rarely emerging beyond the involucre; capsule olive green, borne on a long seta, opening and closing with the dampness of the air; inner cells without semiannular or repand thickenings; outer cells with nodular thickenings or trigones; elater-bearers about 100 with 2 spirals, .6-8 mm long, .005-.007 mm wide; elaters with 3-4 spirals, not interwoven into a central mass, .15-.2 mm long; spores elliptical, greenish, finely papillate, .07-.08 mm long, .035-.045 mm wide; antheridial plants delicate; apex divided into 4 finger-like lobes.

On soil in wet places, or on rocks along rivers. Paradise Valley on Mount Rainier (Frye), 1904; Elwha River Valley in Olympic Mountains (Frye), 1907; Yacolt (Frye), 1911; North side of Orcas Island in San Juan County (Clark), 1923; I.a Push (Frye), 1927.

Montana: Libby (Frye), 1928.

Wyoming: Mt. Washburn in Yellowstone National Park (Frye), 1925.

BLASIA

Plants dark or bluish green, becoming yellow, in tangled mats or in more or less perfect rosettes, closely prostrate or lobes ascending, many times dichotomous, 5-20 mm long, .5-5 mm wide, thalloid to subfoliose; costa present, 5-10 cells thick, becoming gradually thinner to the unistratose margin; margin crenulate, sinuate to deeply lobed; lobes foliose, round, distant to imbricate, incubous; rhizoids numerous, colorless; ventral scales or rudimentary underleaves in irregular rows along costa, ovate, oblong to irregular, attached by posterior margin or rarely at center; margins free; costa-cells elongated, .009-.15 mm long, .03-.036 mm wide; wing cells .03-.06 mm in diameter, rhombic-hexagonal; marginal cells oval to oblong-quadrate, often pointed, .021-.036 mm long; dioicous; antheridial plants more delicate; gemmae of 2 kinds; one kind borne in flask-like receptacles on dorsal surface of costa near apex, oval, flattened, .095-.135 mm long, 3-5 cells wide, bistratose or at margin unistratose; flask-shaped receptacles depending

in number on branch development, 2.4-3.5 mm long, .56-.77 mm wide, their necks at maturity 1.1-2.1 mm long, slender; other kind of gemmae borne on younger plants near apex, not in flash-shaped receptacles, stellate or very coarsely dentate, scale-like, 2 or more cells thick at center, unistratose at margin; archegonia numerous, immersed on dorsal surface; fertilized archegonia covered by an arched and inflated portion of the costa, which is ruptured at the anterior end by the growth of the sporophyte and serves as an involucre; calyptra nearly colorless, membranous; capsule oval, dull brown, 1-1.5 mm long, dehiscing by 4 valves; walls bistratose; inner wall cells with semiannular thickenings; outer wall cells with brown nodular thickenings in cross walls; seta long; spores ovoid, angular, remaining with the elaters as a central mass; elaters with 2 spirals; antheridia several, immersed singly in a row on the dorsal surface of the costa. The only known species is the following.

1. **Blasia pusilla** Linne.

Compared with *Pellia* on page 41.

On wet rocks and by streams. Tacoma (Piper), 1888; Everett (Piper), 1892; Seattle (Piper), 1895; Renton (Frye), 1904; Seattle (Frye), 1907; Olympic Mountains (Frye), 1907; Lester (Frye), 1908; Buck Creek Pass in Glacier Peak Region (Winona Bailey), 1910; Burlington (Clark), 1910 and 1911; Kalama (Frye), 1911; Neah Bay (Rigg), 1911; Olympia (Foster), 1912; Bothell (Frye), 1921; Darrington (Frye), 1928.

Oregon: Mount Hood P.O. (30); Portland (31); Rainier (31); Albany (Van Wert), about 1923.

FOSSOMBRONIA

Plants small, stems fragile, creeping, simple dichotomous, flattened above, convex below, ventral surface with long generally violet colored rhizoids, apex ascending; leaves in 2 rows, succubous, obliquely to horizontally inserted, posterior edge somewhat decurrent, quadrate, broader than long; margins lobed and sinuate, unistratose except at base where 2 or 3 layers thick; cells large, thin walled, filled with chloroplasts; archegonia along midrib on dorsal surface; pseudoperianth narrow at base; mouth wide, lobed, often plicate, cut to base on apical side, surrounded by subulate scales; capsule globose, short-stalked, dehiscing more or less irregularly by 4 valves; wall bistratose, inner layer frequently with incomplete semiannular thickenings; outer

layer of large cells with thin walls and no thickenings; spores large, the layer frequently with incomplete semiannular thickenings; outer layer of large cells with thin walls and no thickenings; spores large, the outer face variously armed; elaters short, bispiral; antheridia on dorsal surface of stem at base of leaves, orange-yellow, naked or covered with scales; gemmae lacking.

- A. Seta about 2 mm long; margin of the spore appearing crenulate; whole spore sides reticulate; heteroicous. 1. *F. dumortieri*
- AA. Seta 8-16 mm long; margin of the spore appearing undulate-serrate; spores crested or papillate or perhaps 1-3 reticulations in the center of the sides; dioicous. 2. *F. longiseta*

Comparison of species of <i>Fossombronia</i>	1. <i>dumortieri</i>	2. <i>longiseta</i>
Length of mature seta in mm.	2	8-16
Spores rough with points, or ridged to form 0-3 or many reticulae.	m	p, 0-3
Apparent number of projections on margin of spore.	16-20	20-40
Margin of spore crenulate or undulate-serrate.	c	u
Mouth of perianth sinuate or dentate-lobed.	s	d
Leaves entire or irregularly lobed or toothed or sinuate-lobed.	i-t-e	s

1. ***Fossombronia dumortieri*** (Huebener & Genth) Lindberg.

Plants in dense pale green patches; stems to 7 mm in length; midrib convex and nearly ovate below; leaves rotund-quadrate, sinuate-lobed, bistratose base passing into unistratose layer; pseudoperianth to 1.7 mm long, mouth sinuate-labed; stalk of capsule about 2 mm long; inner layer of capsule wall with thick incomplete semiannular thickenings; spores brownish-yellow, .035-.045 mm, regularly reticulate, lamellae low, 6-7 areolae across face; areolae 5-6 angled; margin of spores not winged, crenulate with 16-20 teeth; elaters short, broad, pale yellow brown, bispiral.

Damp ground at edge of lake. Sportsmans Lake near Friday Harbor (Frye), 1923, and (Clark), 1925.

2. ***Fossombronia longiseta*** Aust. p. p. Proc. Acad. Nat. Sci. Philad. 1869:228. 1869.

Androcryphia longiseta Austin, Proc. Acad. Nat. Sci. Philad. 1869: 228. 1869.

Stems mostly 6-15 mm long and once dichotomous, rather stout, (15-20 cells in thickness), commonly somewhat tuberously thickened

at apex and perennial through the resumption of apical growth on termination of the dry season, root-hairs vinous-purple; leaves 1.5-3 mm long, subquadrate, assurgent or nearly horizontal, more or less imbricate, irregularly lobed, toothed, or subentire, often of 2-5 layers of cells toward the base; leaf-cells $30-45\ \mu \times 40-60\ \mu$ near the margin, $40-60\ \mu \times 60-150\ \mu$ near the base; monoicous (polyoicous?); involucre usually large, 1.5-3 mm high, campanulate, open to the base on the side toward stem-apex or often connate here forming a complete cup, usually with several subulate squamules adnate to the outer surface, these mostly short but sometimes reaching nearly to the lobate-dentate mouth; seta finally 8-18 mm long; capsule 1-1.2 mm in diameter, the semiannular thickenings of the inner layer of the wall mostly incomplete; spores yellowish-brown, distinctly compressed, $38-50\ \mu$ in maximum diameter, strongly and somewhat remotely cristate, the crests high, projecting $3-6\ \mu$ margin, 20-30 in number in the basilar circumference, more or less obliquely ascending, slightly flexuous, thin, acute, usually undulate-serrulate, unequal in length, disappearing or sparingly confluent at the middle of the face, forming there very rarely 1-3 fully closed meshes; crests sometimes mostly replaced by subacute or truncate spines, these often numerous and crowded, 30-40 in number in the basilar circumference; elaters bispiral, 150-270 μ in length. (Adapted from Howe).

Since this species has been reported by Howe from California and by Macoun from British Columbia, it will probably be found in our area, altho such has not been the case.



Fossombronia longiseta. Three spores showing variability, $\times 305$. (After Howe).

Family J U N G E R M A N N I A C E A E

(Jungermanniaceae Acrogynae)

The vegetative body a bilateral leafy stem thruout, or sexual branches leafy; leaves in 2 rows; stomata none; a third row of leaves (underleaves) either absent or rudimentary or large; archegonia directly transformed from apex of vegetative stem or one of its branches, surrounded by an involucre (perianth) formed from the

union of the leaves of that whorl; leaves (bracts) and underleaves (bracteoles) directly beneath the perianth more or less modified; capsule 4- or rarely 8-valved; elaters always present.

A. Leaves 2-5-lobed to base and the lobes each a single row of cells.

Blepharostoma, p. 128

AA. Leaves 2-5-lobed and the lobes ciliate.

Ptilidium, p. 132

AAA. Leaves otherwise.

B. Leaves not complicate-bilobed or only concavely so.

C. Underleaves smaller than the leaves or scarce or none.

D. Leaves succubously or transversely inserted.

E. Leaves unindented at tip or merely retuse or emarginate.

F. Leaves or their primary lobes entire.

G. Underleaves none or rare or common on the sterile stems, but never present thruout.

H. Valves of the capsule spiral, linear, contorted when open; under leaves common on sterile stems and 2-lobed.

Gyrothyra, p. 65

III. Valves of the capsule straight, lanceolate, not contorted when open; underleaves not common on sterile stems, unlobed in most species.

I. Cell cavity not stellate; perianth terete or merely plicate.

J. Bracts in their lower half somewhat connate with the perianth; rhizoids colorless or occasionally violet.

Nardia, p. 60

JJ. Bracts not connate with the perianth; rhizoids colorless or brownish.

K. All the leaves unindented at tip; underleaves none except in *A. allenii*.

Aplozia, p. 67

KK. Some of the leaves per plant slightly indented at tip; underleaves present but not very common.

Jamesoniella, p. 72

II. Cell cavity markedly stellate on account of the very large rounded trigones; perianth 3-angled with one angle ventral.

Odontoschisma, p. 118

GG. Underleaves present thruout.

L. Trigones bulging into the cells in the older leaves.

Leptoscyphus, p. 93

LL. Trigones not bulging into the cells.

- M. Underleaves deeply bifid, not conspicuous, never connate with the leaves. *Chiloscyphus*, p. 98
- MM. Underleaves rarely bifid, conspicuous, sometimes their base at one side connate with the leaves. *Harpanthus*, p. 102
- FF. Leaves more or less dentate. *Plagiochila*, p. 91
- EE. Leaves 2 or more lobed.
- N. Leaves transversely inserted.
- O. Underleaves from none to common on the sterile stems but not present thruout.
- P. Leaves 2-lobed for $\frac{1}{8}$ - $\frac{1}{2}$ their length; seta of more than 4 rows of external cells.
- Q. Either the trigones in the older leaves bulging into the cells, or the leaf lobes rounded at tip.
- R. Perianth none, the archegonia in the hollowed stem tip. *Gymnomitrium*, p. 55
- RR. Perianth present; uppermost bracts adnate to the perianth. *Marsupella*, p. 57
- QQ. Trigones not bulging into the cells, and in our species the leaf lobes acute. *Sphenolobus*, p. 88
- PP. Leaves 2-lobed for $\frac{1}{2}$ - $\frac{2}{3}$ their length; seta of 4 rows of external cells. *Cephalozella*, p. 104
- OO. Underleaves present thruout. *Pleuroclada*, p. 117
- NN. Leaves succubously inserted.
- S. Leaves with 3-5 principal lobes. *Lophozia*, p. 74
- SS. Leaves with 2 principal lobes.
- T. Underleaves from none to common on the sterile stems but not present thruout, bifid or not; rhizoids scattered.
- U. Leaves 2-lobed for $\frac{1}{10}$ - $\frac{1}{3}$ their length; perianth terete.
- V. Bracts not embracing the perianth, not larger than the leaves. *Gymnocolea*, p. 73
- VV. Bracts embracing the perianth, larger than the leaves. *Lophozia*, p. 74
- UU. Leaves 2-lobed for $\frac{1}{3}$ - $\frac{3}{4}$ their length; perianth 3-angled with one angle ventral. *Cephalozia*, p. 111
- TT. Underleaves present thruout, bifid; rhizoids tufted.

- W. Perianth present, terminal on main branch.
Lophocolea, p. 94
- WW. Perianth none, the archegonia in the end of
 a ventral sac-like branch. *Geocalyx*, p. 103
- DD. Leaves incubously inserted.
- X. Leaves entire or 2-3-lobed for not over $1/6$ their length,
 averaging about .7-1.8 mm long.
- Y. Trigones not bulging into the cells; rhizoids not
 scarce; perianth none, the archegonia in the end of
 a ventral sac-like branch. *Calypogeia*, p. 120
- YY. Trigones in the older leaves bulging into the cells;
 rhizoids scarce; perianth present. *Bazzania*, p. 123
- XX. Leaves 3-4-lobed for $1/3$ - $1/2$ their length, averaging
 about .4 mm long. *Lepidozia*, p. 126
- CC. Underleaves about the same size as the leaves and abundant.
- Z. Leaves 2-lobed for $1/4$ - $1/3$ their length; leaf cells 28-63 μ ;
 underleaves from unlobed to 2-lobed for $1/6$ their length.
Hygrobiella, p. 116
- ZZ. Leaves 2-lobed for $1/2$ - $3/4$ their length; leaf cells 18-30 μ ;
 underleaves 2-lobed for $1/2$ - $3/4$ their length.
Anthelia, p. 131
- BB. Leaves sharply complicate-bilobed.
- a. Ventral lobe of leaf not saccate.
- b. Underleaves none.
- c. Dorsal leaf-lobe the smaller or the two equal; leaves
 not incubously inserted, the lobes not entire except
 in one species.
- d. Dorsal and ventral lobes of the leaves both oblong;
 leaf base often apparently with a vein; perianth
 terete and plicate. *Diplophyllum*, p. 135
- dd. One or both of the leaf lobes shorter than oblong;
 leaf base with no sign of vein; perianth dorsiven-
 trally compressed. *Scapania*, p. 139
- cc. Dorsal leaf-lobe the larger; leaves incubously inserted,
 the lobes entire. *Radula*, p. 153
- bb. Underleaves present thruout.
- e. Underleaves not bilobed; elaters 2-3-spiral; plants com-
 monly 3-10 cm long. *Madotheca*, p. 157
- ee. Underleaves bilobed; elaters 1-spiral; plants commonly
 1-2 cm long. *Lejeunea*, p. 163
- aa. Ventral lobe of leaf saccate; elaters 1-spiral.
Frullania, p. 164

 Comparison of the genera of Jungermanniaceae

-
1. Leaves sharply complicate-bilobed.....
 2. Ventral lobes of leaves sac-like.....
 3. Leaves 3-5-lobed and the leaves ciliate.....
 4. Leaves 2-4-lobed nearly to base and the lobes each a single row of cells....
 5. Underleaves present thruout, of roughly the same area as the leaves, and ,
2-lobed for about $\frac{2}{3}$ their length.....
 6. Leaves incubous
 7. Species forming perianth.....
 8. Perianth terete or merely plicate, or 3-angled with one angle dorsal, or ven-
trally or laterally compressed, or 4 or 5 angled, or flattened frontally...
 9. Seta of 4 rows of cells externally.....
 10. Leaves 2 or more lobed, or entire to emarginate.....
 11. Underleaves about the same area as the leaves and common on sterile stems
 12. Leaves succubously or transversely inserted.....
 13. Leaves complicate-bilobed, and both dorsal and ventral lobes oblong.....
 14. Underleaves present thruout, or common, rare or none on sterile stems....
 15. Leaves or their primary lobes normally entire.....
 16. Lower half of the bracts somewhat connate with the perianth.....
 17. Trigones bulging into the cells at least in older leaves.....
 18. Leaves unlobed, altho some per plant slightly retuse to emarginate.....
 19. Underleaves common on sterile stems and bilobed.....
 20. Bracts larger than the leaves.....
 21. In leaves not acutely complicate-bilobed the sinus angular, crescentic or none
 22. Leaf lobes acute, obtuse, rounded or none.....
 23. Number of spirals in the elaters.....
 24. Elaters trumpetshaped and attached by small end near valve tip, or neither
trumpetshaped nor attached.....
-

	Lophozioideae							
	Gymnomitrium p. 53	Geocalyx p. 103	Plagiocchia p. 91	Nardia p. 60	Gyrothya p. 65	Aplozia p. 67	Jamesonella p. 72	Leptoscyphus p. 83
1.	-	-	-	-	-	-	-	-
2.	-	-	-	-	-	-	-	-
3.	-	-	-	-	-	-	-	-
4.	-	-	-	-	-	-	-	-
5.	-	-	-	-	-	-	-	-
6.	-	-	-	-	-	-	-	-
7.	-	-	+	+	+	+	+	+
8.	×	×	t	t	t	t	t	t-1
9.	-	-	-	-	-	-	-	-
10.	l	l	e	e	e	e	e	e
11.	-	-	-	-	-	-	-	-
12.	t	s	s	t	t	s-t	s	s
13.	-	-	-	-	-	-	-	-
14.	n	t	r	r-c	r	n-c	r	t
15.	+	+	-	+	+	+	+	+
16.	×	×	-	+	-	-	-	-
17.	±	-	-	±	+	±	-	+
18.	-	-	-	±	-	-	+	±
19.	-	+	-	-	+	-	-	±
20.	+	-	-	+	-	±	+	-
21.	a	c	n	n-c	n	n	c	n
22.	a-r	a	n	n-o-r	n	n	n-r	n
23.	2-4	2	2	2	2	2	2	2
24.	n	n	n	n	n	n	n	n

CUT ALONG THIS LINE

Lophozioideae								Ceph- aloz- iell- oideae
	Chiloseyphus p. 98	Harpanthus p. 102	Lophocolea p. 94	Gymnocolea p. 73	Lophozia p. 74	Marsupella p. 57	Sphenolobus p. 88	Cephalozella p. 104
1.	-	-	-	-	-	-	-	-
2.	-	-	-	-	-	-	-	-
3.	-	-	-	-	-	-	-	-
4.	-	-	-	-	-	-	-	-
5.	-	-	-	-	-	-	-	-
6.	-	-	-	-	-	-	-	-
7.	+	+	+	+	+	+	+	+
8.	l	t	d	t	t	t	t	t-4-v +
9.	-	-	-	-	-	-	-	
10.	e	e	l	l	l	l	l	l
11.	-	-	-	-	-	-	-	-
12.	s	s	s	s	s	t	t	t
13.	-	-	-	-	-	-	-	-
14.	t	t	t	r	rct	n	n-r	n-c
15.	+	+	+	+	±	+	±	±
16.	-	-	-	-	-	+	-	-
17.	-	-	-	-	±	±	-	-
18.	+	+	-	-	-	-	-	-
19.	+	-	+	-	±	-	-	±
20.	-	-	-	-	+	+	+	+
21.	n-c	n-c	c	a	a-c	a-c	a-c	a
22.	o-r	o-r	a-r	o	a-r	o-r	a	a
23.	2	2	2	2	2	2	2	2
24.	n	n	n	n	n	n	n	n

Cephalozioideae								Ptilidi- oldene
	Cephalozia p. 111	Pleuroc'ada p. 117	Hygrobiella p. 116	Odontoschisma p. 118	Calyptogeia p. 120	Bazzania p. 123	Lepidozia p. 126	Anthelia p. 131
1.	-	-	-	-	-	-	-	-
2.	-	-	-	-	-	-	-	-
3.	-	-	-	-	-	-	-	-
4.	-	-	-	-	-	-	-	-
5.	-	-	-	-	-	-	-	+
6.	-	-	-	-	+	+	+	-
7.	+	+	+	+	-	+	+	+
8.	v	v	v	v	×	v	v	t
9.	-	-	-	-	-	-	-	-
10.	l	l	l	c	e	e-l	l	l
11.	-	-	+	-	-	-	-	+
12.	s	t	t	s	×	×	×	t
13.	-	-	-	-	-	-	-	-
14.	n-r	t	t	r	t	t	t	t
15.	+	+	-	+	+	+	+	-
16.	-	-	-	-	×	-	-	+
17.	-	-	-	+	-	+	-	-
18.	-	-	-	-	±	±	-	-
19.	-	-	+	-	+	+	±	+
20.	+	-	-	-	-	-	+	+
21.	c	a	a	n	n-a-c	n-a-c	a	a
22.	a	a	a-o	n	n-o-r	n-a-o	a	a
23.	2	2	2	2	2	2	2	2-3
24.	n	n	n	n	n	n	n	n

CUT ALONG THIS LINE

Ptilidioideae			Scapanioideae		Raduloidae	Madothecoideae	Jubuloideae	
	Riepharostoma p. 128	Ptilidium p. 132	Diplophryllum p. 135	Scapania p. 139	Radula p. 153	Madotheca p. 157	Lejeunea p. 163	Frullania p. 164
1.	-	-	+	+	+	+	+	+
2.	-	-	-	-	-	-	-	+
3.	-	+	-	-	-	-	-	-
4.	+	-	-	-	-	-	-	-
5.	-	-	-	-	-	-	-	-
6.	-	-	-	-	+	+	+	+
7.	+	+	+	+	+	+	+	+
8.	t	t	t-5	t-f	t-f	t-d	5	v
9.	-	-	-	-	-	-	-	-
10.	1	1	1	1	1	1	1	1
11.	+	-	-	-	-	-	-	-
12.	t	t	t	s	×	×	×	×
13.	-	-	+	-	-	-	-	-
14.	t	t	n	n	n	t	t	t
15.	+	-	-	±	+	±	+	+
16.	-	-	-	-	-	-	-	-
17.	-	+	-	-	-	±	-	-
18.	-	-	-	-	-	-	-	-
19.	±	±	-	-	-	-	+	+
20.	+	-	-	+	-	-	-	-
21.	a-c	a	×	×	×	×	×	×
22.	a	a	a-r	a-r	o-r	a-r	o-r	a-r
23.	2	2	2	2	2	2-3	1	1
24.	n	n	n	n	n	n	t	t

GYMNOMITRIUM

Plants bright or glaucous green or reddish brown, densely caespitose; stems rigid, ascending or erect, or prostrate with ascending apex, sparingly dichotomous, often canaliculate along dorsal surface on drying; subfloral innovations present; sterile stems same width thruout; fertile stems swollen at tips; flagella always present; leaves succubous, transversely inserted, imbricate, in upper part closely so, symmetrically appressed; basal leaves often destroyed, strongly concave, subcomplicate-bilobed; keel round or obtuse; sinus in our species 1/6 to 1/4 leaf-length, acute; margin crenulate by projecting cells; hyaline border sometimes extending nearly to center of leaf; cells small, thin-walled; trigones none or minute; cuticle densely and minutely granulate or verruculose; underleaves wanting thruout; dioicous or monoicous or rarely synoicous; archegonial inflorescence terminal; bracts several pairs, larger than leaves, bilobed, with hyaline teeth; inner pair small; perianth none; involucre the swollen tip of the stem; calyptra free or adnate to the perigynium tube; androecium terminal, clavate or capitate; bracts similar to leaves but more concave; antheridia 1—2, oval.

Comparison of species of Gymnomitrium and Marsupella	Gymnomitrium		Marsupella			
	1. concin- natum	2. obtusum	ustulata p. 58	emarginata p. 59	sulcivittil p. 60	phacelata p. 58
Leaves with hyaline border.....	+	+	—	—	—	—
Perianth present.....	—	—	+	+	+	+
Spores smooth or verruculose.....	v	v	s	s	s	s
Leaf margin entire or roughened by projecting cells.....	c-r	r	c	c	c	c
Hyaline leaf border <i>broad, narrow or wanting</i>	n	b	w	w	w	w
Length of green leaf-cells in mu.....	26-40	15-27	12-18	6-28	25-33	21-28
Plants <i>aquatic or terrestrial</i>	t	t	t	t	t	a
Leaf widest above its middle.....	—	—	—	—	—	+
Leaf-lobes <i>acute, obtuse or rounded</i>	a	o-r	a	o	o-r	r
Trigones <i>large or small</i>	l	s	s	l	l	s
Marginal row of leaf-cells larger than others.....	—	—	—	—	+	+
Proportional depth of leaf-notching....	1/6-1/4	1/6-1/4	1/4-1/3	1/6-1/4	1/3-1/2	1/4-1/3
Dorsal leaf-margin recurved.....	+	+	—	+	—	—
Cortical stem cells larger than interior				+	+	+
Cortical stem cells thick-walled.....				+	—	—
Plants <i>brownish, reddish, green, purplish or whitish</i>	w-b	w-r	p-b	b-r	r-p	g-r

- A. Leaves strongly concave; hyaline border narrow; sinus acute; apex of lobes acute; margins entire (crenulate in var. *intermedium*). 1. *G. concinnatum*
- AA. Leaves slightly concave; hyaline border extending nearly to center of leaf; sinus obtuse or acute and closed; apex of lobes obtuse; margins distinctly crenulate. 2. *G. obtusum*

1. ***Gymnomitrium concinnatum*** (Lightfoot) Corda.

Plants densely caespitose or mixed with mosses, glaucous green at tips of stems, but otherwise bright green or tinged with red or reddish brown; stems sparingly branched, 1.5-15 mm long, leafless at base; sterile stems same width thruout; sexual stems with swollen tips; leaves transversely inserted, closely imbricate, very concave, oval to broadly ovate, bilobed; sinus $1/6-1/4$ the length of the leaf, acute; apex of lobes acute; margin entire; hyaline border narrow; cells 26-40 μ long, 15-27 μ wide; median cell walls thin, with large trigones; hyaline cells with confluent trigones; cuticle granulate; dioicous; inflorescence terminal on main stem; bracts 3-4 pairs, similar to leaves but larger, more concave, closely imbricate, sinus small, margin reflexed; inner bracts delicate, irregularly toothed or lobed, borders involute; archegonia several; androecium terminal on main stem; bracts similar to leaves but more concave; antheridia slightly elliptical; capsule small, brown, emersed; spores small, brown, verruculose.

Queets River valley in Olympic Mountains (Frye), 1907.

2. ***Gymnomitrium obtusum*** (Lindberg) Pearson.

Plants growing in caespitose or closely compressed mats or scattered among mosses, yellowish brown or bright green or branches and stem-tips reddish brown; stems sparingly branched, on drying canaliculate along dorsal surface; leaves concave, transversely inserted, broadly ovate or oval when spread out, closely imbricate and symmetrically appressed, bilobed, with broad hyaline border, green from base to only a little past middle; sinus $1/6-1/4$ leaf-length, broadening upward; margin crenulate by projecting cells, especially in upper part; cell walls thin; green cells 15-27 μ , with small but distinct trigones; hyaline cells 12-14 μ , with uniformly thickened walls and trigones; cuticle minutely verruculose; archegonial inflorescence borne at apex of main stem; outer bracts 3-4 pairs, similar to leaves in shape, their apices truncate and somewhat reflexed; inner bracts

more delicate, irregular in shape, variously lobed, subacute to obtuse, sinuses shallow, margin crenulate by projecting cells and papillae; archegonia numerous; androecial inflorescence terminal on main stem; bracts numerous, imbricate, similar to leaves but more delicate in texture, lobes with reflexed margin; capsule dark, only slightly exerted; spores small, brown, minutely verruculose; elaters with 2 spirals, brown.

On shaded rocks. Snoqualmie Pass in Cascade Mountains (probably Piper), 1891; Mt. Rainier (Allen), 1904; Queets River valley in Olympic Mountains (Frye), 1907; Mt. Constitution (Roberts), 1925; Darrington (Frye), 1928.

Montana: Mt. Trilby (40).

MARSUPELLA

Plants small and delicate to large and coarse, usually densely caespitose, appearing compressed dorsiventrally; stems erect or ascending, rarely prostrate, subsimple or dichotomous, sending out stolons or nearly leafless flagella from near base of stem; rhizoids often wanting except at base on stolons; leaves succubous, erect or spreading, bilobed, opposite, more or less concave, subcomplicate-carinate, transversely inserted (in our species); underleaves wanting; monoicous or dioicous; archegonial inflorescence terminal on main stem; bracts 2-4 pairs, larger and less deeply lobed than leaves, innermost pair adnate to the lower part of the perianth; sinus of bracts shallow; upper part of stem a round involucre formed by stem-tip; perianth delicate, included in bracts, after escape of capsule 4-6-lobed; capsule with numerous brown thickenings in walls; elaters with 2 spirals.

A. Plants aquatic; leaf widest above its middle. 1. *M. sphacelata*

AA. Plants terrestrial or rupestral; leaf widest at or below its middle.

B. Leaf lobes acute; trigones small.

2. *M. ustulata*

BB. Leaf lobes obtuse to rounded; trigones large.

C. Marginal row of leaf cells not larger than the others; leaves notched for $\frac{1}{6}$ - $\frac{1}{4}$ their length; dorsal leaf margin recurved; cortical cells of the stem not larger than the interior ones, thick-walled.

3. *M. emarginata*

CC. Marginal row of leaf cells larger than the others; leaves notched for $\frac{1}{3}$ - $\frac{1}{2}$ their length; dorsal leaf margin not recurved; cortical cells of the stem larger than the interior ones, thin-walled.

4. *M. sullivantii*

Species compared with *Gymnomitrium* on page 55.

1. *Marsupella ustulata* Spruce.

Plants in broad purplish brown to nearly black patches; stems 2-5 mm long, suberect, simple or with a few branches, sometimes innovating from below the inflorescence; rhizoids numerous, colorless; leaves of lower part of fertile branches and those of sterile branches little imbricate, erect or erect-spreading, twice as wide as the stem, .31-.40 mm long, broadly oval, bilobed for $1/4$ - $1/3$ their length; sinus about a right angle, angular; lobes acute or subacute; leaf cells 12-18 μ , walls almost equally somewhat thickened; trigones rarely distinct except on the bracts; paroicous; female inflorescence on a clavate branch; subinvolucral bracts rather abruptly much larger and broader than the leaves, cordate at base, bilobed for $1/8$ - $1/5$ their length, sinus acute, lobes usually obtuse; bracts of male inflorescence $1/3$ or more connate, lobes most commonly obtuse; antheridia 2-3, oval, on a stalk of the same length; perianth much shorter than the bracts and $1/3$ connate with them, ovate; mouth small, crenulate; capsule spherical, reddish brown, without semiannular thickenings; spores 9-12 μ , pale reddish brown, nearly smooth; elaters bispiral, reddish brown, nearly equalling the spores in width. (Adapted from MacVicar).

Oregon: Mt. Hood (45).

We have not seen the material, and so far as we are aware it is the only report of the species from our area.

2. *Marsupella sphacelata* (Giesecke) Dumortier, Recueil d'Observ. Jungerm. p. 24. 1835.

Plants in tufts, dull green and usually tinged with brown above; stems 2.5-4 cm long, thick, flaccid, pale, simple or with few branches, with a tuft of innovations from below the female inflorescence; cortical stem cells hyaline, thin walled, twice as large as the interior cells; rhizoids colorless or violet, scarce on stolons as well as on stems; lower leaves distant, mostly destroyed; upper subimbricate, larger, erect-spreading, embracing and crossing the stem, round-quadrate to round-cordate, bilobed for $1/4$ - $1/3$ their length; sinus acute, open; lobes rounded at tip; margin plane, entire; leaves on sterile stems and innovations hardly larger upward, oblong-quadrate, subimbricate; leaf cells 21-28 μ , 5-6-angled; marginal row thin-walled, pale; trigones small but distinct; dioicous; involucral bracts very broad, involute, the margin frequently plicate in the middle, bilobed for $1/3$ their length, tips of the lobes rounded; cells in cross section of seta about

equal in size, 20-30 forming the periphery. (Adapted from MacVicar and K. Mueller).

We have seen no material of this from our region, and since we find no detailed description of the sporophyte it seems to be comparatively unknown.

Montana: Lake McDonald, Sperry Glacier, (40).

3. *Marsupella emarginata* (Ehrhart) Dumortier.

Plants green, yellowish or reddish brown or sometimes purple, forming loose or densely caespitose mats; stems simple or subsimple, stout, 1-3 cm long, erect; rhizoids wanting except at base of stolons, colorless; leaves firm, strongly concave or subcomplicate, distant or approximate, at stem-apex imbricate, when spread out quadrate or nearly quadrate-orbicular, .3-.9 mm in diameter, smooth; base broad and embracing half the stem, without marginal row of cells; margin entire; apex bilobed; sinus $1/6-1/4$ leaf length; lobes as well as the sinuses obtuse; cells round to hexagonal, 6-28 μ , marginal cells a little smaller; triangular trigones present; dioicous; archegonial inflorescence terminal on main stem; bracts 2-4 pairs, gradually becoming larger than the leaves but similar to them; perianth immersed and the innermost bracts adnate to it, mouth 4-6-lobed; androecium terminal on main stem; bracts 2-4 pairs, closely imbricate, somewhat similar to leaves; antheridia 3-4, large, oval, borne on long stalk; capsule brown, spherical; spores brown, smooth; elaters brown, with 2 spirals.

M. emarginata may be mistaken for *M. bolanderi* which has not been found in Washington. It is distinguished by the smaller size, the dark color, obliquely inserted leaves which are distinctly succubous, and the larger (16-36 μ) cells, the always marginate bracts, the more exserted perianth-like involucre, and the few antheridia to a bract.

On rocks or exposed banks. Easton (Roell), 1888; Cascade Mountains (Piper), 1891; Stevens Pass, in Cascade Mountains (Sandberg & Leiberger), 1893; Paradise Valley on Mount Rainier (Frye and Flett), 1904; Olympic Mountains (Frye), 1907; Pacific Beach (Foster), 1910; Mt. Ellinor (Foster), 1912; Olympic Hot Springs (Foster), 1914; Friday Harbor (Clark), 1925; Darrington (Frye), 1928.

Oregon: Mt. Hood (29, 31).

1. **Nardia obovata** (Nees) Lindberg.

Plants green or reddish brown, forming thick tufts or creeping among mosses; stems suberect or prostrate; branches subventral, arising from axils of leaves; rhizoids long, reddish purple, numerous, arising from base of leaves at perianth; leaves obliquely inserted (45°), subimbricate to imbricate, slightly decurrent on dorsal side, distant at base of stem, plane or concave, longer than broad, .5-.7 mm wide, .6-.8 mm long, obovate to ovate from a sheathing base, obscurely if at all marginate; underleaves none except in association with bracts, apex rounded; margin entire; cells pentagonal or rounded, a little flaccid and thin walled, 32-40 μ ; cuticle punctate to coarsely striate-papillate; cells at margin sometimes quadrate making leaf obscurely marginate; trigones small, distinct; monoicous; archegonial inflorescence terminal on main stem; bracts similar to but larger than leaves, adnate to lower half of perianth; bracteoles absent; perianth immersed in the bracts, visible $\frac{1}{3}$ its length by recurving of the bracts, oval or obovate, upper parts 5-6-plicate; perianth-mouth contracted, small, lacinate and denticulate; antheridia below perianth; bracts more complicate, saccate at base; antheridia oval; spore brown, 16-20 μ ; elaters brown, with 2 spirals.

Subalpine species found in Europe, England, Scotland and Ireland as well as in America. Hamilton (Foster), 1905; North Bend (Frye), 1926.

Montana: Swiftcurrent Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

2. **Nardia rubra** (Gottsche) Evans, Bryologist 22:54, figs. 1-7. 1919.

Jungermannia rubra Gottsch, in Bolander, California Med. Gaz. 1870:184.
Also Underwood, Bot. 13:113, pl. 4. 1888.

Plants green or reddish brown, forming thin mats; stems 3-12 mm long, .3-.35 mm wide, prostrate or ascending at apex, simple or rarely laterally branched; rhizoids colorless, long, numerous; leaves obliquely inserted, slightly or not at all decurrent, distant to imbricate, rounded or ovate or suborbicular, on sterile stems .35-.79 mm long, on fertile stems .5-1.3 mm long and .6-1.5 mm wide, red or tinged with red, distinctly margined by a row of larger thick-walled cells, entire; underleaves none; cells 20-50 μ ; trigones distinct; walls thick; cuticle punctate; dioicous; archegonial branch with crowded leaves, suberect, reddish purple; bracts larger than leaves, marginate, upper pair adnate to perianth; perianth exerted $\frac{1}{2}$ - $\frac{2}{3}$ its length, red or

purple, lower portion 2 cells thick; perianth mouth abruptly contracted into a short beak, at first denticulate, later lacerate; calyptra red or purple, unistratose at apex; androecium terminal; bracts 3-10 pairs; antheridia ovoid, in pairs, short-stalked, accompanied by a few paraphyses; capsule dark brown, ovoid; wall bistratose; seta quite long; spores brown, 13-16 μ , very finely granulate; elaters brown with 2 spirals, attenuate at ends, .09-.13 mm long.

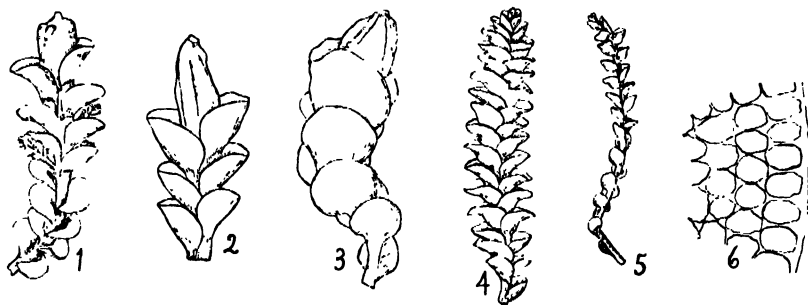
On moist exposed banks. Tacoma (Roell), 1888; Olympia (Henderson), 1891; Renton (Frye), 1904; Tacoma (Flett), 1905; Hamilton (Foster), 1905; Houghton (Frye), 1909; Ilwaco (Frye), 1909; Kalama (Frye), 1911; Pacific Beach (Foster), 1911; Rolling Bay (Foster), 1911; Aberdeen (Foster), 1911; Lake Crescent (Foster), 1911; Skykomish (Frye), 1925; North Bend (Frye), 1926.

Oregon: Cape Arago (Frye), 1922.

Idaho: Bovil (Clark), 1925.

Montana: Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928; Libby (Frye), 1928.

According to Evans (23) Pacific Coast reports of *N. crenulata* should be referred to *N. rubra*.



Nardia rubra. 1, 2. Plants with perianth, dorsal view, $\times 7.5$. 3. Plant with perianth, lateral view, $\times 7.5$. 4, 5. Male plants, mostly dorsal view, $\times 7.5$. 6. Marginal cells from near tip of stem leaf, $\times 132$. (After Evans).

3. *Nardia scalaris* (Schrader) Gray.

Plants forming reddish brown mats or mingled with mosses; stems creeping or ascending, 2-5 mm long, simple, slightly laterally compressed; rhizoids numerous, colorless; leaves imbricate, orbicular or suborbicular, .6-.9 mm long, .7-.8 mm wide, concave, entire or slightly retuse, without differentiated marginal cells; underleaves present, large, triangular-subulate, entire, acute; cells 36-50 μ , round or hexagonal; walls thin; trigones very large; cuticle smooth; dioicous;

archegonia terminal on main stem; bracts 2, broadly orbicular, larger than stem leaves, entire or sometimes emarginate; bracteoles triangular-subulate, connate to bracts at lower portion; perianth extending $2/3$ its length beyond bracts, numerous, lower half adnate to bracts, widest a little above middle, its mouth contracted; androecium terminal or at middle of stem; bracts closely imbricate, somewhat smaller than leaves; antheridia 2, oval, small; spores brown; elaters brown.

Nardia scalaris differs from *N. compressa* in that the latter has broader and more compressed leaves, and triangular, small, dentate underleaves.

In loose mats, on wet clay banks or wet rocks. Mount Rainier at 7000 feet (Allen), 1900; Paradise Valley on Mount Rainier (Flett), 1904; Olympic Mountains (Frye), 1907; Aberdeen (Foster), 1911; Pacific Beach (Foster), 1911.

4. *Nardia geoscypha* (De Notaris) Lindberg.

Plants brownish green or rarely green, in caespitose mats or mixed with mosses; stems creeping or their tips ascending; fertile stems fleshy, 2-4 mm. long; sterile stems slender, terete, radiculose; branches lateral; rhizoids numerous, colorless; leaves obliquely inserted; those on fertile stems closely imbricate, broadly ovate, concave, entire or emarginate, saccate, without a marginal row of different cells; those on sterile stems distant to subimbricate, subvertical, orbicular, not marginate, sometimes bilobed and then the segments are acute; underleaves lanceolate, minute or fugaceous except in the inflorescence, usually wanting on sterile stems; leaf cells 20-40 μ , round or hexagonal; walls thin; trigones large; cuticle smooth; paroicous; archegonial inflorescence terminal on main stem, immersed; stem apex hollowed out into a small rudimentary sac extending downward at nearly right angles to stem; bracts larger than leaves, 3-4 pairs, irregularly lobed or crispate at margins, emarginate, acute, increasing in size toward perianth; innermost bracteoles large, irregularly lobed or bilobed and trilobed, round, some small and indistinct; perianth not extending beyond the bracts, delicate, contracted at mouth; mouth subentire or denticulate; antheridia borne in axil of archegonial bract; spores brown, 16 μ , very minutely verruculose.

Subalpine. Mount Rainier (Piper), 1895, (Flett), 1908 and (Foster), 1909.

Montana: Libby (Frye), 1928.

5. *Nardia breidlerii* (Limpricht) Lindberg.

Plants reddish brown or purple, in thick patches; stems ascend-

ing, 2-3 mm long, bent; branches lateral; rhizoids numerous, generally colorless, sometimes purplish; leaves a little broader than long or orbicular, .16-.19 mm long, twice as broad as the stem and curved toward it, generally bordered by a row of differentiated cells at margins, bifid to $\frac{1}{3}$ - $\frac{1}{4}$ their length, upper leaves sometimes retuse; underleaves small, lanceolate, with 2 tooth-like lobes; leaf cells small, 10-16 μ , without or with small trigones; cuticle more or less smooth; all walls sometimes equally thickened; dioicous; archegonia borne at apex of main stem, or terminal on principal branch; archegonia 2-4; neck composed of 6 layers of cells; perianth fleshy, hollow, saccate on ventral side; bracts inserted on upper half of perigynium, broadly orbicular, more concave than leaves; bracteoles usually lanceolate; involucre at first concealed by delicate crenulate cells, later becoming 4-lobed; antheridial branches short, thickly leaved; bracts round, often with a basal tooth, those of the dorsal side plicate; antheridia 2-4; stalk of 2 layers of cells half as long as the large round body, 6-7 stalk-cells to a row; capsule brown, round, .34 mm long, .27 mm wide; walls bistratose; spores brown, smooth 10 μ .

On wet soil. Mt. Rainier at 6300 feet (Allen), year (?); Paradise Valley on Mt. Rainier (Foster), 1909.

Montana: Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928.

An arctic and alpine species not elsewhere known from North America, but widely distributed in Europe, and known also from Siberia.

GYROTHYRA

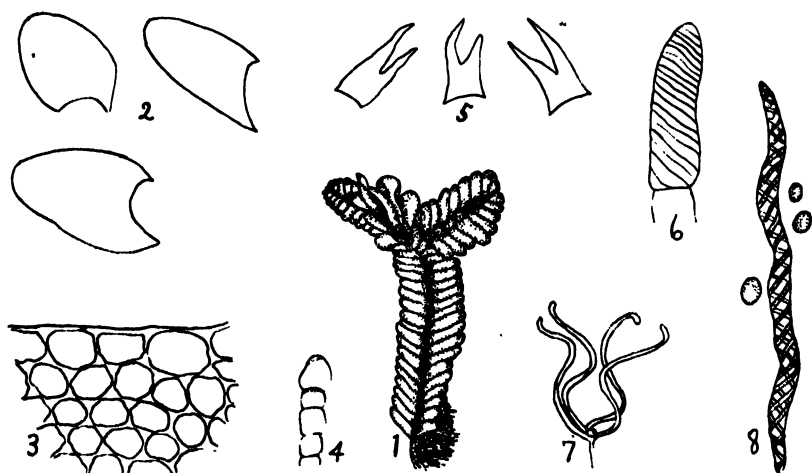
Plants subsimple, foliose; stems creeping, sparingly branched; leaves succubous, entire; underleaves present, free, cleft deeply into 2 subulate segments; trigones large and triangular; cuticle striate; dioicous; archegonial inflorescence terminal on main stem; bracts 2 pairs, united to perianth at its center; androecial spikes terminal when young, later becoming median; capsule long, cylindric, extending beyond perianth, dehiscing spirally by 4 long narrow valves; walls without spiral thickenings; elaters with 2 spirals, free, blunt at ends; spores minutely papillate. There is only the following species.

1. **Gyrothyra underwoodiana** Howe, Bull. Torr. Bot. Club 24:202. 1897.

Species compared with *Nardia* on page 61.

Plants light green or reddish, in caespitose mats; stems thick,

ascending, 1-3 cm long, 2-4 mm wide, sometimes a little dorsiventrally compressed, simple or with lateral branches, subfloral innovations present; rhizoids numerous, forming a thick felt, long, straw colored and tinged with red, arising at base of leaves from linear red callosities; leaves obliquely inserted, subimbricate to imbricate, oval, 1.7-3 mm long, 1.4-2 mm wide, a little decurrent dorsally, those at apex of stem margined with a row of differentiated cells forming a border; underleaves present, on older portions of stem hidden by rhizoids, purple, 2 cleft for $\frac{1}{2}$ - $\frac{1}{3}$ their length into subulate segments, acute; leaf cells pentagonal or hexagonal, pellucid, 30-80 μ ; marginal cells quadrate, oblong, often twice as large as the median cells; dioicous; archegonial branch terminal on main stem; perigynium nearly at right angles to the stem; bracts 2-4 pairs, entire, repand, similar to stem leaves, more or less concealing the perianth; the upper pair inserted on perianth or about its middle; bracteoles inconspicuous, subentire; perianth free for about $\frac{1}{3}$ - $\frac{1}{2}$ its length; its upper portion nearly free of chlorophyll, subtubular; lower portion more saccate or inflated; mouth crenulate; androecia on more slender plants; bracts saccate; antheridia elliptical, in axils of bracts; capsule linear, 3-6 mm long; valves slender, attached spirally to a hyaline disc, wide-spreading when open; elaters .21-.42 mm long, 12-15 μ wide; spores yellowish brown, 12 μ , minutely papillate.



Gyrothya underwoodiana. 1. Female plant, $\times 2.5$. 2. Three leaves, $\times 9$. 3. Cells along leaf margin, $\times 112$. 4. Cross section of leaf margin, $\times 108$. 5. Three underleaves, $\times 12$. 6. Surface view of very young capsule, $\times 50$. 7. Open capsule, moist, showing 4 valves, $\times 6$. 8. Elaters and 3 spores, $\times 137$. (After Howe).

On wet soil. Snoqualmie Pass (Piper), year (?); Montesano (Heller), 1898; Hoquiam (Foster), 1900; South Bend (Frye), 1907; Ilwaco (Frye), 1907; Mt. Constitution (Wentworth), 1923; North Bend (Frye), 1926.

Oregon: Albany (Van Wert), about 1922.

This species is distinctly a Pacific Coast one, first found in California.

APLOZIA (Haplozia, Jungermannia)

Plants 2-8 cm long; stems ascending to erect or creeping, simple or bearing a few lateral branches, often with subfloral innovations from beneath perianth; rhizoids numerous, long, colorless; leaves succubous, alternate, inserted transversely or obliquely or longitudinally, oblong-elliptic or oblong-ovate or orbicular, never lobed; margins entire throughout; underleaves none (except in *A. allenii*); dioicous or monoicous; androecium terminal or median; bracts entire, similar to leaves; antheridia 1-3, stalked, with or without sterile hairs; archegonia terminal on main stem; bracts similar to leaves, distinct from each other and from the perianth; perianth cylindric, clavate, plicate in upper part or very abruptly contracted into a short beak, now and then somewhat compressed laterally; calyptra free, surrounded at base by sterile archegonia; capsule oval or globose, dehiscing by 4 straight valves; inner cell-wall with semiannular thickenings; seta long; elaters with 2 spirals.

- A. Underleaves present, fugaceous or large. 1. *A. allenii*
- AA. Underleaves none.
 - B. Leaves round or wider than long. 2. *A. sphaerocarpa*
 - BB. Leaves longer than wide.
 - C. Plants large, 2-8 cm; trigones none. 3. *A. cordifolia*
 - CC. Plants smaller; trigones present.
 - D. Perianth abruptly contracted at apex into a short beak; paroicous. 4. *A. lanceolata*
 - DD. Perianth not abruptly contracted at apex into a short break; dioicous.
 - E. Plants 2-5 mm long; cell-walls but slightly pigmented, cells 26-35 μ . 5. *A. riparia*
 - EE. Plants .3-1.5 mm long; cell-walls deeply pigmented, cells 18-28 μ . 6. *A. atrovirens*

Comparison of species of Aplozia	1. allenii	2. sphaerocarpa	3. cordifolia	4. lanceolata	5. riparia	6. atrovirens
Underleaves none, undivided or 2-parted	u-p	n	n	n	n	n
Leaves longer than wide.....	+	-	+	+	+	+
Leaves unnotched, retuse or emarginate.	u-e	u-r	u	u	u	u
Trigones none, small or large.....	l	s	n	l	s	s
Trigones bulging into the cells.....	-	-	-	+	-	-
Cuticle striate, smooth or rough.....	t	m	t	t	m-r	m
Perianth fusiform, pyriform, obovate, clavate or cylindrical.....		o-c	f	y-c	p	p
Perianth abruptly contracted into short beak.....		+	-	+	-	-
Dioicous or paroicous.....	d	p	d	p	d	d
Length of plants in cm.....	1.5-3	1-3	2-8	3-5	3-1.5	2-3
Median leaf cells in mu.....	20-30	25-35	27-45	24-42	26-35	18-28
Rhizoids colorless, brown or violet.....	c	c-v	c	c-b	c	c
Marginal row of leaf cells different in color or size, or in neither.....	c	n-c-s	s	s	s	s

1. *Aplozia allenii* (Clark) new comb.

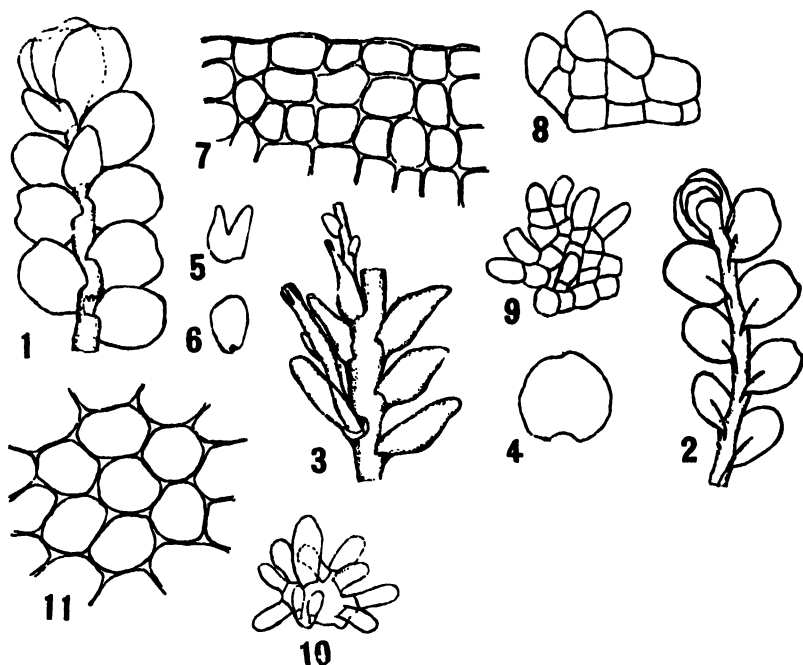
Jungermannia allenii Clark, Bull. Torrey Bot. Club. 36:303. 1909.

Plants brownish green or reddish, growing in tufts; stems 1.5-3 cm long, .15-.25 mm in diameter, ascending or suberect, sparingly branched, the branches arising close to the ventral end of the line of attachment of the leaves; rhizoids few or none, not pigmented; leaves distant to subimbricate, obliquely inserted, somewhat concave, slightly decurrent, oval to subrotund, 1-1.4 mm long, .8-1.35 mm wide, undivided or slightly emarginate, entire, bordered by a row of more deeply pigmented cells; underleaves sometimes fugaceous and minute, sometimes large and persistent, mostly 20-40 μ in length and bearing numerous hyaline papillae; the large ones occasionally attaining a length of 1 mm, sometimes undivided, sometimes variously bilobed or bifid; median leaf-cells 20-30 μ ; trigones large and distinct; cuticle striolate; dioicous.

The specimens examined are all sterile with the exception of a single plant bearing a very immature female inflorescence. On the basis of this plant the species is assumed to be dioicous. Unfortunately in the absence of mature floral organs the generic position cannot be

definitely determined. The reddish pigment which is sometimes very marked points perhaps to *Nardia* or *Jamesoniella*, but is considered wisest to retain the species in *Aplozia* at least for the present.

On rocks, more or less submerged. Paradise Valley on Mt. Rainier (O.D. Allen), year (?), (Flett), year (?) and (Foster), 1909.



Aplozia allenii. 1. Ventral view, $\times 15$. 2. Dorsal view, $\times 15$. 3. Part of stem with 2 branches, $\times 15$. 4. Leaf, $\times 15$. 5, 6. Underleaves, $\times 140$. 7. Cells from leaf margin, $\times 240$. 8. Underleaf, $\times 240$. 9, 10. Underleaves showing papillae, $\times 140$. 11. Cells from middle of leaf, $\times 240$. (After Clark).

2. *Aplozia sphaerocarpa* (Hooker) Dumortier.

Plants in compact tufts, pale green or brown; stem 1-3 cm long, erect or ascending, simple; rhizoids numerous, long, colorless or somewhat violet; leaves soft, concave, orbicular or sometimes retuse at apex, decurrent at dorsal margin; cell 25-35 μ , smaller toward the margin, 4-6-angled; walls thin; trigones usually small but distinct; marginal row of cells quadrate, not or hardly larger than the second row, frequently hyaline-brown, forming a somewhat distinct border; cuticle smooth; paroicous; perianth obovate or clavate, $1/2$ - $2/3$ exserted, 3-6-angled above, smooth below; apex shortly tubular; mouth

crenulate; spores 16-20 μ , reddish-brown, finely papillate; elaters 8-10 μ thick, reddish brown. (Adapted from MacVicar).

Pacific Beach (Foster), 1911; Mt Angeles near Port Angeles (Frye), 1927.

Wyoming: Yellowstone National Park (45) as *Jungermannia tersa*.

3. *Aplozia cordifolia* (Hooker) Dumortier.

Plants dark or yellowish green, in mats or creeping among mosses; stems vigorous or flaccid, erect or prostrate, 2-8 cm long, branching frequently; rhizoids few, colorless; lower stem-leaves subimbricate, clasping the stem; upper stem-leaves distant, rotund, often broader than long, .81-1.4 mm in diameter, not decurrent dorsally; apex round; margin entire; underleaves wanting thruout; leaf-cells round hexagonal; apical cells 18-30 μ ; median cells 27-45 μ , basal cells 72-96 μ , thin-walled, deeply pigmented; trigones none; cuticle delicately striate; dioicous; archegonia terminal on main stem; bracts 2-3 pairs, similar to the leaves but more concave, closely imbricate; perianth cylindric, gradually contracted at apex, its mouth with 4-8 denticulate lobes; androecium lacking; capsule oval, on a short stalk; spores brown, 24 μ ; elaters brown, short, bispiral.

On wet rocks in streamlets. Olympia (Henderson), 1891; Mt. Rainier (Allen), 1900 and (Flett), 1904; Queets and Elwha river valleys in Olympic Mountains (Frye), 1907.

Oregon: Mt. Hood (30).

Montana: Blackfoot Glacier (40); Swiftcurrent Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

Wyoming: Wolf Creek in Sheridan County, Centennial Hills in Albany County, La Plata Mine in Albany County, (42).

4. *Aplozia lanceolata* (Schrader) Dumortier.

Plants in light green tufts or among mosses; stem erect or creeping, 3-5 cm long; sparingly branched by forking, rarely with subfloral innovations; rhizoids numerous, colorless or brownish; leaves imbricate, alternate, obliquely inserted, decurrent dorsally; apex rounded; margin entire; cells round to subquadrate; marginal ones 21-27 μ ; median ones 24-42 μ ; basal ones 45-60 μ long and 27-30 μ wide; thin walled; basal cells richly filled with chlorophyll, median and marginal cells less so; trigones large; cuticle coarsely striate; paroicous or rarely monoicous; archegonial inflorescence terminal on main

stem; bracts free, entire, similar to leaves; perianth cylindric, abruptly contracted at apex into a short depressed beak; antheridia beneath archegonial bracts or on subfloral innovations; capsule oval; wall of 2 layers of cells; spores brown, smooth, tetrahedral..

No gemmiferous plants were found in our material. Gemmae are described as being 1-2-celled, elliptic, borne at the ends of small-leaved stolons or among the perigonal bracts.

Along river courses. Easton (Roell), 1888; Cascade Mountains (Allen), 1900; Roy (Allen), 1901; near Humes Glacier in Olympic Mountains (Frye), 1907.

Idaho: Moscow Mountain (Clark), 1923.

Montana: Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928; Polson (Frye), 1928.

5. **Aplozia riparia** (Taylor) Dumortier.

Plants dark green, in densely caespitose mats; stems erect or creeping among mosses, .03-1.5 cm long; subfloral innovations present, often bearing numerous flagella, arising from dorsal side of the leaf axil, rarely with latero-ventral branches; rhizoids numerous, colorless; leaves imbricate, alternate, obliquely inserted, horizontal, spreading, broadly ovate or oval, .8-1.2 mm long, .7-.9 mm wide; underleaves none; leaf-cells 26-35 μ ; trigones present, minute, very distinct; walls not pigmented or very slightly so; cuticle smooth or rough; dioicous; archegonial plants more or less like sterile forms, perianth terminal on main stem; bracts similar to the leaves but larger; perianth projecting 2/3 its length, fusiform or oblong, slightly frontally compressed, with deep furrow on the anterior side, laterally with 2 longitudinal folds; perianth-mouth plicate with 5-9 folds, contracted, and lacinate; androecia small; perichaetial bracts terminal, erect imbricate, slightly complicate, saccate at base, slightly larger than leaves.

Foot hills of Mount Rainier (Allen), 1905; Lake Crescent (Foster), 1911; Friday Harbor (Clark), 1925; Darrington (Frye), 1928.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928; Polson (Frye), 1928.

6. **Aplozia atrovirens** (Schleicher) Dumortier.

Plants dark or yellowish green, densely caespitose, stem erect or creeping among other mosses, .2-.5 cm long; subfloral innovations or branches from ventral axil of leaves; rhizoids numerous, colorless; leaves imbricate, alternate, obliquely inserted, spreading or ascending, broadly ovate or oval, .85-.95 mm long, .7-.8 mm wide, entire; apex

rounded; underleaves none; leaf cells round to hexagonal, 18-42 μ long, 18-24 μ wide; walls thin, deeply pigmented; trigones present, small to large, distinct or indistinct; cuticle smooth; dioicous; archegonial inflorescence terminal on main stem; bracts similar to leaves but larger; bracteoles wanting; perianth extending about 2/3 beyond bracts, oblong-ovate, slightly frontally compressed, upper part deeply plicate; its mouth constricted, lacinate; androecium terminal on main stem; bracts smaller than the leaves but similar in shape, erect, imbricate, slightly complicate, saccate at base; antheridia round and single, with short stalks; capsule long-pedicelled, globular.

We could find no stolons on the Washington material.

On wet rocks. Headwaters of Elwha River in Olympic Mountains (Frye), 1907; Aberdeen (Foster), 1909, 1911; Brinnon (Foster), 1911; Dosewallips River (Foster), 1911; junction of White and Greenwater rivers (Frye), 1926.

JAMESONIELLA

Plants comparatively large, often reddish yellow or purple; stems ascending or erect, with incurved apex, often rigid, with innovations from below the female inflorescence; leaves succubous, obliquely inserted almost half way around the stem, erect-connivent in the upper part of the plant, ovate to somewhat rounded or kidneyshaped, entire; trigones often large; underleaves minute, evanescent and thus often wanting except in the involucre; dioicous; involucre bracts larger than the leaves, more or less lacinate; bracteoles large, lacinate, somewhat united with the bracts; perianth large, long exerted when fertile, oblong-ovate to cylindrical, somewhat contracted at the mouth, deeply 4-10-plicate above; male bracts 4-6 pairs, terminal, ventricose, with 1-2 teeth on the dorsal margin; antheridia solitary; capsule oval to elliptical; wall of 4 cell layers, the 3 inner with semiannular and annular thickenings, the outer with knob-like thickenings; spores small, finely warty; elaters bispiral.

1. *Jamesoniella autumnalis* (De Candolle) Stephani.

Jungermannia rauana Stephani, Spec. Hep. 2:73. 1901.

Comared with *Gymnocolea*, *Sphenobolus* and *Lophozia* on page 76.

Plants in dark green or yellowish green flat patches, somewhat reddish toward the tip; stems 1-4 cm long, prostrate with ascending tips, simple or branched, innovating from below the female inflorescence; branches arising from the ventral angle of the leaves;

rhizoids colorless to near apex of stem; leaves succubous, imbricate, slightly secund, inserted diagonally; older leaves horizontal or slightly secund, oblong-oval; upper leaves erect-appressed, rotund-oval, convex, entire or commonly retuse, decurrent dorsally; underleaves subulate, 2-5 cells wide, from half to almost as long as the leaves, evanescent and thus commonly only on young parts; leaf cells 25-36 μ , rounded polygonal; marginal row smaller, oblong-quadrate, with thicker walls; trigones rather small but distinct, not bulging into the cells; cuticle smooth; dioicous; bracts of the involucre erect but apex squarrose, oblong to oblong-rotund; apex entire to emarginate; margin usually somewhat toothed near base, sometimes entire; bracteoles large, lacinate, commonly attached to the bract; fertile perianth long-exserted, almost cylindrical but slightly clavate, smooth below, 4-5-plicate above; mouth long and unequally ciliate; sterile perianth hardly or slightly exserted, oval, plicate; capsule oval; spores 11-15 μ , reddish brown; elaters reddish brown. (Adapted from MacVicar and K. Mueller).

In Stephani's *Species Hepaticarum* 2:73, 1901, it is reported from "Washington Terr." by Rau.

Montana: Polson (Frye), 1928.

Macoun reports it from Banff, Alberta. We have seen only the Polson plants.

GYMNOCOLEA

Plants with the habit of *Lophozia*, dark green to almost black; stems prostrate, with few rhizoids, little or not at all branched; leaves oblique and succubous when old, nearly transverse when young, not decurrent, narrow at base, bilobed, the lobes usually obtuse; wall of leaf cells thin or firm; trigones none or small; underleaves seldom present, awl-shaped, not lobed; gemmae unknown, but the sterile perianths break off and produce new plants; dioicous; involucre bracts spreading from the perianth, smaller or at least not larger than the leaves but otherwise resembling them; bracteoles small, lanceolate; perianth very large, clavate-pyriform, smooth, not plicate; mouth narrow, dentate; antheridia solitary in the leaf axils; stalk of the sporophyte of as large cells outside as inside; capsule cylindrical, somewhat pointed, its wall of 2 layers of cells.

1. *Gymnocolea inflata* (Hudson) Dumortier.

Compared with *Jamesoniella*, *Sphenolobus* and *Lophozia* on page 76.

Plants green or yellowish brown, with a somewhat oily lustre.

forming closely interwoven mats; stems creeping or ascending, 5-30 mm long, sparingly subdichotomous or with a few lateral branches or subfloral innovations; rhizoids few, short, colorless or yellow; leaves distant or contiguous, obliquely inserted, horizontal-spreading or erect-spreading, orbicular-ovate or quadrate-oblong, slightly decurrent dorsally, plane or concave, .98-1.2 mm long, .84-1.33 mm wide, bilobed to $\frac{1}{4}$ - $\frac{1}{3}$ their length; sinuses narrow, obtuse; margin entire or slightly repand; lobes obtuse, rarely inclined toward each other; underleaves wanting except in association with archegonial bracts; leaf cells round or hexagonal, 24-40 μ long, thick-walled; trigones very indistinct; cuticle smooth or obscurely striate; dioicous; archegonia terminal; bracts similar to leaves but a little smaller, 2 pairs; perianth much exposed and often to the base, elliptic or elongated-pyriform, inflated, plicate, with sometimes 2 longitudinal folds, obtuse at apex, its mouth 4-5-lobed and toothed; capsule elongated-oval, on short seta; spores 15-20 μ in diameter, papillate; elaters contorted, slightly attenuated, .12-.18 mm long; antheridial plant more slender; bracts terminal, in 4-6 pairs, transversely inserted, broader than long, concave; antheridia single, globose-oval, short-stalked.

In peat bogs. Hamilton (Foster), 1904.

Wyoming: Norris Geyser Basin in Yellowstone National Park (Frye), 1925.

LOPHOZIA

Plants small to robust; stems creeping or ascending, simple or dichotomous, with a few lateral branches, sometimes with subfloral innovations; rhizoids generally numerous; leaves succubous or transversely inserted, alternate, 2-5-lobed, plane or dorsally concave, sometimes subcomplicate-bilobed, never actutely so; underleaves wanting, or when present mostly small, lanceolate-subulate, entire, bifid or ciliate-fringed; cell walls thin to thickened; trigones wanting to large and triangular; archegonia terminal on main stem; bracts distinct, larger than but similar to leaves, often with more lobes, margin sometimes dentate; perianth oval or clyndric or cylindric-obovoid, plicate above the middle or obscurely so at the mouth; perianth apex obtuse, more commonly conical or abruptly contracted to a small mouth; calyptra free; androecium terminal or median; bracts sometimes with an additional tooth or lobe on the dorsal margin near the ventricose base; antheridia 1-9, mostly short-stalked, with or without paraphyses; capsule subglobose to elongated-ovoid; dehiscing by 4 straight rigid

valves, usually composed of 2 layers of cells, inner with semiannular thickenings, elaters with 2 spirals.

A. Leaves bidentate.

B. Underleaves present.

C. Upper leaves gemmiferous and deformed. 3. *L. heterocolpos*

CC. Gemmae absent.

D. Stems to 3 cm long; leaves slightly decurrent; parioicous.

4. *L. kaurini*

DD. Stems to 5 cm long; leaves strongly decurrent; dioicous.

2. *L. bantriensis*

BB. Underleaves absent or rarely a few present.

E. Stems 12 mm long; translucent; cell walls thin; trigones generally present; gemmae absent.

1. *L. badensis*

EE. Stems larger (5 cm); plants dark and opaque if small; either cell walls thick, or gemmae present, or both.

F. Lobes rounded-obtuse.

15. *L. obtusa*

FF. Lobes acute or pointed.

G. Stems thick; plants bluish green; margins of upper leaves spinose-dentate.

9. *L. incisa*

GG. Stems thin; plants green, not bluish green; margins entire.

H. Leaf sinuses crescentic, shallow; leaves brown or green, flaccid; broadest below middle; gemmae reddish.

8. *L. alpestris*

HH. Leaf sinuses acute or subobtusate, about 1/5-1/2 the leaf-length; leaves green or reddish; not flaccid.

I. Leaves squarrose with attenuated lobes; cell walls very thin; gemmae reddish brown.

5. *L. longidens*

II. Leaves not squarrose; lobes not attenuated; gemmae absent or green.

J. Leaf cells with small trigones; mouth of perianth dentate; usually growing on rocks.

6. *L. ventricosa*

JJ. Leaf cells with large trigones; mouth of perianth lobed, ciliate-dentate; usually growing on soil.

7. *L. porphyroleuca*

Comparison of species of <i>Jamesoniella</i> , <i>Gymnocolea</i> , <i>Sphenolobus</i> and <i>Lophozia</i>	Jame- soniell.	Gymno- colea
	autumnalis p. 72	inflata p. 73
Usual number of primary lobes or divisions of the leaves	0-2	2
Underleaves constantly present, or none to few	f	f
Trigones bulging into the cells	—	—
Involucral bracts larger than the leaves	+	—
Leaves very nearly transversely inserted	—	—
Tips of leaf lobes <i>acute</i> , <i>obtuse</i> , <i>rounded</i> , <i>apiculate</i>	r	r
Gemmae common, uncommon, none	n	n
Involucral bracts embracing the perianth	+	—
Upper leaves commonly cross-gemmiferous at tip	—	—
Sinus between leaf lobes <i>crescentic</i> or <i>angular</i>	c	a
Except for primary lobing, leaves <i>entire</i> , <i>toothed</i> , <i>ciliate</i> at base	e	e
Leaves <i>squarrose</i> , at about a <i>right angle</i> , or distinctly <i>less</i>	r-l	r-l
Cilia at base of leaf margin of cells much <i>longer</i> than wide, or about as long	g	l
Sinus between leaf lobes <i>greater</i> or <i>less</i> than a right angle	a-y	p-ol
Perianth <i>pyriform</i> , <i>clavate</i> , <i>cylindrical</i> , <i>ovate</i> or <i>oval</i> , <i>obovate</i> , <i>oblong</i>	i	ld
Mouth of perianth <i>dentate</i> , <i>crenulate</i> , <i>ciliate</i> , <i>lobed</i>	d	d
Paroicous or dioicous	25-36	24-30
Cells in mu	t	m
Cuticle of leaf <i>smooth</i> , <i>granulate</i> , <i>verruculose</i> , <i>striate</i>		

Sphenolobus			Lophozia					
michaui p. 89	exsectus p. 91	minutus p. 89	9. Incisa	5. longidens	6. ventricosa	1. badensis	8. alpestris	15. obtusa
2	2	2	2	2	2	2	2	2
f	f	f	f	f	f	f	f	f
-	-	-	-	-	-	-	-	-
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	-	-	-
a-p	a	a-p	a	a	a	a-o	a-o	r
c	c	c	c	c	c	n	c	u
-	+	+	+	+	+	+	+	+
-	+	-	-	-	-	-	-	-
a	c	a	a	c	c	a	c	a
e	t	e	t	e	e	e	e	e
r	r-l	l	l	s	r-l	r-l	r-l	r-l
l p-a	l o-y	g y	l b	g a-b	g o-l	l y	g y-l	l a-y
l d 10-20 v	i-d d 8-17 v	ldi d 12-18 v	id d 27-54 m	ild d 24-30 m	d d 20-30 m	r d 30-35 m-t-v	d d 18-33 m	id d 24-30 v-t

CUT ALONG THIS LINE

Lophozia

7. porphyro-leuca	8. hetero-colpos	2. hantrensis	4. kaurini	10. lycopod-oides	11. hatcheri	12. floerkei	13. attenuata	14. barbata
2	2	2	2	3-5	3-4	3-5	3-4	3-4
f	c	c	c	c	c	c	f	f
+	+	-	-	-	-	-	-	-
+	+	+	+	+	+	+	+	+
+	-	-	-	-	-	+	+	-
a	a	a-o	a	p-o	p-o	a-o	a	a-o
n-c	c	n	n	u	c	n-u	c	u
+	+	+	+	+	+	+	+	+
-	+	-	-	-	-	-	+	-
a	a	c	a	a	a	a	a	a
e	e	e	e	c	c	c	e	e
l	r	r-l	r	l	l	r-l	l	l
l-g o-l	l o-l	g y	g y	l l-g o-l	l l o	a g o-y	g ol-y	l o-l
ild d 24-45 m	rd d 24-30 v	i d 35-42 v-t	i p 34-42 v	i d 15-36 m	d a 18-30 v	i d 18-27 v	i d 18-20 v-t	ld d 15-36 g

AA. Leaves 3-5 lobed.

K. Stems with upright flagelliform shoots with closely appressed leaves; gemmae usually abundant. 13. *L. attenuata*

KK. Stems without flagelliform shoots.

L. Cilia present at base of ventral margin of leaves.

M. Plants 5-30 mm long, with 1-2 short cilia at base of leaves; cells of cilia about as long as broad; leaves 3-lobed to $\frac{1}{3}$ their length; lobes broadly triangular.

12. *L. floerkei*

MM. Plants 4 cm or less long, with 5-10 long cilia at base of leaves; cells of cilia longer than broad.

N. Leaves 3-4-lobed; lobes with a spinose tooth at apex; gemmae present.

11. *L. hatcheri*

NN. Leaves 4-5-lobed; lobes broadly triangular; usually mucronate; gemmae rare.

10. *L. lycopodioides*

LL. Cilia absent at base of leaves.

O. Lobes of leaves toothed; leaves strongly crispate when dry.

9. *L. incisa*

OO. Lobes of leaves entire; leaves little altered in drying.

P. Lobes obtuse; gemmae rare.

14. *L. barbata*

PP. Lobes frequently with a spinose tooth at apex; gemmae frequent.

11. *L. hatcheri*

1. ***Lophozia badensis*** (Gottsche) Schiffner.

Plants in thin pale green or yellowish green mats; stems creeping or ascending, 4-12 mm long, translucent, simple or sparingly branched, sometimes with subfloral innovations; rhizoids numerous, long, colorless or brownish, to apex of stem; leaves approximate or imbricate on upper stem, obliquely inserted, more or less erect, rarely horizontal, concave, quadrate to round-ovate, base broad and shortly decurrent, those on sterile stems rectangular, bilobed for $\frac{1}{4}$ - $\frac{1}{3}$ their length, sinus acute; lobes acute, rarely obtuse; cells 30-35 μ , 4-6-angled; walls thin; trigones small; cuticle smooth or finely striate-verruculose; underleaves wanting, sometimes a few present and rudimentary; dioicous; bracts erect, closely embracing the perianth, round-ovate to quadrate bilobed for $\frac{1}{6}$ - $\frac{1}{5}$ their length, one or both sometimes with a third small lobe; sinus acute; lobes acute; perianth exserted, cylindrical, slightly plicate in upper part, mouth contracted, rostellate, crenulate with long cells; capsule oval, reddish brown; spores reddish brown, 11-15 μ , verruculose; elaters dark reddish

brown; antheridia several pairs at middle of stem, bracts erect, dorsal lobe with a tooth or 3-lobed.

On rocks. North side of Orcas Island (Clark), 1923; Friday Harbor (Clark), 1925.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

2. *Lophozia bantriensis* (Hooker) Stephani.

Plants in large tufts, reddish brown or green; stems 2-8 cm long, flexuous, ascending to suberect, simple or with subfloral innovations; rhizoids near apex, few, long, brown or colorless; leaves large, flaccid, more or less undulate, secund or horizontal, uppermost suberect, subrotund, margin decurrent, bilobed for $\frac{1}{6}$ - $\frac{1}{5}$ their length; sinus shallow, broad, usually gibbose; lobes triangular, obtuse, sometimes acute, unequal; cells 35-42 μ , large at base, smaller at margin, round-polygonal; walls thin; trigones small; cuticle striate-verruculose; underleaves large, lanceolate to subulate, more or less lacinate-dentate; dioicous; involucre bracts resembling leaves, narrow, nearly transverse, concave, entire; perianth long-exserted, cylindrical, smooth, more or less plicate at apex; mouth contracted, rostellate, shortly and unequally ciliolate; capsule oval; spores 13-16 μ , verruculose, red; elaters dark.

On rocks. Friday Harbor (Daughterly), 1923.

• Oregon (23).

3. *Lophozia heterocolpos* (Thedenius) Howe.

Plants in green or light green patches, or mixed with mosses; stems 15 mm long, ascending to erect, simple, sparingly branched, with subfloral innovations; rhizoids numerous, long, brownish; leaves imbricate, erect, more or less secund dorsally, round to oval, bilobed for $\frac{1}{4}$ - $\frac{1}{3}$ their length; margin shortly decurrent; sinus narrow, acute or obtuse, gibbose and recurved; lobes unequal, obtuse, sometimes rounded and acute; cells 24-30 μ , round-polygonal, opaque; walls thin; trigones large; cuticle roughened; underleaves oval-lanceolate, with 1-3 dentate-ciliate teeth on each side or bifid with long divergent segments; dioicous; involucre bracts transverse, erect, rotund-ovate, concave, undulate; sinus narrow, acute; lobes acute or obtuse; perianth long-exserted, oblong-ovate, smooth, apex contracted; mouth very shortly rostellate, irregularly crenate-dentate; gemmae at apex of deformed depressed leaves on attenuated shoots, brown, 2-celled.

On rocks. North side of Orcas Island (Clark), 1923.

Montana: Libby (Frye), 1928.

4. **Lophozia kaurini** (Limpricht) Stephani.

Plants in green or yellow green mats with mosses; stems to 2.5 cm, suberect, simple, with subfloral innovations; rhizoids numerous, long, brownish to end of stem; leaves imbricate, horizontal or secund dorsally, oblong-quadrate, margin shortly decurrent, bilobed for $1/5-1/4$ their length; sinus variable, broad, obtuse, gibbose; lobes unequal, acute, sometimes sharp-pointed, obtuse or rounded; cells $34-42\ \mu$, round-polygonal, larger and oval at base; walls thin; trigones rather small; cuticle coarsely verruculose; underleaves subulate to lanceolate, sometimes with 1 or more teeth at margin; paroicous; antheridial bracts 4-6 pairs, larger than leaves, transversely inserted, imbricate erect, concave, saccate at base; sinus strongly gibbose, rotund-ovate to oblong-ovate, lower margin sometimes with a small lobe; antheridia oval-globose, short stalked, in pairs; perianth long exserted, cylindrical, smooth; mouth contracted, more or less long rostellate, shortly and unequally ciliolate.

On rocks. Friday Harbor (Clark), 1923.

5. **Lophozia longidens** (Lindberg) Macoun.

Plants dark green, in loose tufts or mixed with mosses, tinged with brown; stems 1-3 cm long, ascending to suberect, with subfloral innovations; rhizoids long, colorless, scattered to near apex; leaves spreading, slightly oblique, half embracing the stem, channelled and concave below, flat or convex above, squarrose, ovate-quadrate to ovate-rectangular, slightly decurrent, bilobed for $1/5-1/3$ their length, a few 3-lobed; sinus obtuse, lunate, not gibbose; lobes narrowly triangular, acute, straight, slightly divergent; cells $24-30\ \mu$; walls thin; trigones minute; cuticle smooth; gemmae in clusters at tips of lobes of upper leaves, reddish or yellowish brown, 2-celled, many-angled; underleaves wanting; dioicous; bracts resembling leaves in size, erect-spreading, irregularly 2-5-lobed, margin with short teeth; lobes narrow and acute; bracteoles variable, more or less ovate and dentate; perianth long exserted, obovate-clavate, plicate in upper part; mouth with several small lobes, dentate-ciliate, teeth 1-3 or rarely 6 cells long; capsule oval-oblong, yellowish brown; spores $10-13\ \mu$, verruculose, yellowish brown; elaters reddish brown; antheridial plants branched, densely leaved, leaves erect-spreading; bracts 6-8 pairs, imbricate, transverse, broad and saccate at base; antheridia 2, oval-globose.

On decaying wood. Moscow Mountain, Idaho, (Clark), 1923.

6. **Lophozia ventricosa** (Dickson) Dumortier.

Plants yellowish green or sometimes reddish brown, densely caespitose on rocks; stems creeping or ascending, .5-1.5 mm long, sparingly branched, ventral surface of stem reddish; rhizoids numerous, long, colorless; leaves approximate to subimbricate, older ones obliquely inserted, younger ones transversely inserted, spreading or subvertical, slightly concave, subcomplicate, somewhat flaccid, ovate-quadrate, .8-1 mm long, .7-.9 mm wide, divided for $1/5$ - $1/3$ their length into 2 subequal lobes; sinus broad, obtuse; lobes ovate-triangular, subobtuse or acute; margin entire, never reflexed; underleaves none; leaf cells round or hexagonal, 24 - $36\ \mu$, thin-walled; trigones small, distinct; cuticle smooth or indistinctly roughened; gemmae abundant, irregular, somewhat tetrahedral, mostly 2-celled, commonly at leaf apex, sometimes making margin erose; dioicous; archegonia terminal on main stem; bracts somewhat larger than leaves, the inner ones more deeply and unequally 3-4-lobed, slightly plicate; lobes subobtuse; perianth cylindric-ovate, 1-celled except at extreme base, upper part plicate, its mouth ciliate-denticulate; androecium terminal; bracts imbricate, transversely inserted, subcomplicate, ventricose; antheridia single or in pairs, oval, on long stalk; paraphyses few; capsule brown, ovate; valves 3 layers of cells thick; spores yellowish brown, finely papillate, 12 - $14\ \mu$; elaters fusiform-subglobose, .08-.13 mm long.

On rocks in moist places. "Rigi" at Lake Cle Elum (Roell), 1888; Mt. Rainier (Piper), 1895; Ashford (O.D. Allen), 1900; Cascade Mountains (Allen), 1900; Trout Lake near Mt. Adams (Frye), 1925.

Oregon: Mt. Hood (29, 31).

Idaho: Moscow Mountain (Clark), 1924; Craig Mountain (Clark), 1924.

Montana: Sperry Glacier region (40); Piegan Pass and Iceberg Lake trails from Many Glaciers in Glacier National Park (Frye), 1928; Whitefish (Frye), 1928.

Wyoming: Near Giant Paint Pot in Yellowstone National Park (Frye), 1925.

7. **Lophozia porphyroleuca** (Nees) Schiffner.

Plants green or reddish brown, caespitose or creeping, on soil; stems erect or prostrate, 3-10 mm long, simple or forked, ventral side

of stem reddish; rhizoids long, numerous, colorless; leaves distant to subimbricate, transversely inserted, alternate, erect-spreading, subcomplicate, orbicular, .5-.8 mm long, divided $1/5$ - $1/3$ their length into 2 subequal lobes; lobes triangular-ovate, acute; margin entire, reflexed or ruffled, never dentate; sinuses obtuse and spreading; underleaves wanting, rarely present, subulate, .16-.2 mm long, .08-.16 mm wide; leaf cells round or hexagonal, 24-45 μ ; walls thin, often pigmented; trigones large, triangulate; cuticle smooth or papillose; our material totally without gemmae; dioicous; archegonia terminal on main stem; bracts 2 pairs, similar to leaves but larger, more complicate, 3-lobed; sinuses obtuse; margin undulate; perianth cylindric, 1-1.5 mm long; mouth plicate, lobate; lobes numerous, acute, ciliate-dentate; androecium terminal; antheridia short-stalked, 2-3 in a bract-axil; capsule brown, elliptic, 1.1-1.25 mm long; spores brown, papillose, 8-12 μ ; elaters brown, with 2 spirals..

On logs and soil. Paradise Valley on Mt. Rainier (Piper), 1895; Queets River valley about half a mile from Queets-Elwha pass in Olympic Mountains (Frye), 1907; Friday Harbor (Clark), 1925; Mt. Angeles near Port Angeles (Frye), 1927.

Oregon: Seaside (31).

Idaho: Moscow Mountain (Clark), 1923.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

8. *Lophozia alpestris* (Schleicher) Evans.

Plants in bright green or brownish green caespitose mats or mixed with mosses; stems 5-10 mm long, creeping, ascending at apex, simple or sparingly branched; rhizoids numerous, long, colorless or sometimes colored at base; leaves transversely inserted, or horizontal above, more or less erect, round-quadrate, narrowest at apex, bilobed for $1/10$ - $1/7$ their length; sinus broad, crescentic; lobes triangular or ovate, acute or obtuse or more or less incurved; margin entire or undulate, reflexed; gemmae in brown masses on leaves at apex of stem, mostly irregular or stellate, 1-2-celled; leaf cells round-hexagonal, 18-33 μ ; walls usually brownish and thickened; trigones distinct, delicate to large; cuticle smooth; underleaves rarely a few, but wanting in connection with bracts; dioicous; archegonia terminal on main stem; bracts larger than leaves, sharply 2-3-lobed; perianth cylindric, smooth, toward mouth plicate or 4-lobed; androecium terminal or at some distance from apex; bracts similar to leaves but more complicate, saccate at base; antheridia round or oval, single, on long stalk;

capsule round-oval, violet-reddish brown; spores golden brown, scarcely wider than elaters.

Elwha River valley in Olympic Mountains (Frye), 1907; Paradise Valley on Mt. Rainier (Foster), 1909.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928; Polson (Frye), 1928.

9. *Lophozia incisa* (Schrader) Dumortier.

Plants bright to dark green, caespitose or creeping; stems erect or prostrate, 3-8 mm long, .27-1.9 mm wide, simple or once dichotomous, rarely with 2 or more branches near apex; rhizoids numerous, long, colorless; leaves imbricate, crowded at apex, alternate, transversely inserted, subcomplicate, quadrate to ovate-oblong, .9-1 mm long, .9-1.5 mm wide, divided $\frac{1}{3}$ - $\frac{1}{2}$ their length into 2-3 unequal lobes; lobes triangular-ovate, acute; margin reflexed, toothed; sinuses acute or rounded; underleaves absent except in association with bracts; leaf cells quadrate-hexagonal 27-54 μ , thin-walled; trigones distinct; chlorophyll gathered at center of cell; cuticle smooth; gemmae frequent, in clusters at leaf tips, irregularly tetrahedral; dioicous; archegonia terminal on main stem; bracts 3-5-cleft, larger than leaves, broader than long, dentate, strongly crisped; perianth ovate to elongate-obovoid, bistratose at base; mouth plicate, ciliate-dentate; androecium terminal; bracts closely crowded, similar to leaves; antheridia single or in pairs, round, short-pedicelled; capsule reddish brown, subglobose; its valves thick, rigid; spores brown, 13-18 μ , minutely papillate; elaters fusiform, with 2 spirals, .11-.15 mm long, 8-10 μ wide.

On wet ground or decaying logs. Mt. Rainier (Allen), 1900; Seattle (Frye), 1904; Mt. Rainier (Frye and Flett), 1904; Cathlamet (Foster), 1907; Liberty Creek in Spokane County (Bonser), 1907; Queets River valley in Olympic Mountains (Frye), 1907; Lacenter (Davis), year (?); Westport (Foster), 1908; Pacific Beach (Foster), 1910, 1911; Buck Creek pass in Glacier Peak region (Winona Bailey), 1910; Olympic Hot Springs (Foster), 1914; Friday Harbor (Clark), 1925; Olga (Clark), 1925; North Bend (Frye), 1926; La Push (Frye), 1927.

Oregon: Mt. Hood (29).

Idaho: Moscow Mountain (Clark), 1925; Bovil (Clark), 1925; Grizzly Camp (Clark), 1927.

Montana (38); Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928.

10. *Lophozia lycopodioides* (Wallroth) Cogniaux.

Plants large and robust, green or brownish, densely caespitose; stems 4 cm long, firm, sparingly branched, with subfloral innovations; rhizoids dense, colorless; leaves appressed, obliquely inserted or at apex subtransversely inserted, distinctly explanate, alternate, concave, subrotund, at ventral base with 5-10 long cilia, at dorsal base auriculate with a fifth small lobe, from sinuses radiately plicate, 4-lobed to $\frac{1}{4}$ their length; apices incurved; sinuses shallow; lobes subequal, broad and obtuse, or 3 lobes apiculate with the fourth acute, or all lobes apiculate; underleaves present thruout, large, deeply bifid into ciliate lobes; cells 25 μ , basal ones 54 μ long and 27 μ wide; trigones large, at base fewer; cuticle smooth; dioicous; archegonia terminal; bracts transversely inserted, similar to leaves, more deeply cleft into 4-5 acute lobes; bracteoles similar to leaves but larger and more ciliated; perianth long exserted, oval or clavate, 7-9-plicate, obtuse; mouth lobate; male inflorescence terminal; bracts ventricose, deeply 4-lobed, the lobes incurved; antheridia 4-9, long-stalked; capsule subglobose, brown, long-stalked; spores 14 μ ; elaters .15 mm long, brown. (Adapted from Stephani).

Easton, and at "Rigi" at Lake Cle Elum, (45).

Montana: Holzinger Basin, Avalanch Basin, (40); Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

Wyoming: Yellowstone National Park (45).

11. *Lophozia hatcheri* (Evans) Stephani.

Plants in bright green mats or creeping among mosses; stems 5-20 mm long, simple or sparingly branched; rhizoids long, numerous, colorless; leaves approximate or distant, very obliquely inserted, alternate, horizontal-quadrate or broader than long, .7-.75 mm long, .8-.9 mm wide, divided $\frac{1}{5}$ - $\frac{1}{4}$ their length into 3-4 subequal lobes; sinuses obtuse, spreading or acute; lobes ovate-triangular; with a spinate tooth at apex; margin entire, except sometimes ventral margin with 1-3 cilia, reflexed; underleaves large, deeply bifid, longly ciliate; leaf cells round to hexagonal, 18-30 μ ; walls thick, firm; trigones large, distinct, triangular; cuticle faintly striate; gemmae numerous, as golden brown spots on lobes of leaves, irregularly triangular or quadrate, 1-2-celled; dioicous; involucre bracts with several lobes, the lobes ending in long cilia; male bracts terminal or below the apex, in 5-7 pairs, imbricate, concave, the lobes incurved, saccate at base, asymmetrical, the dorsal lobes smaller; antheridia 2-5, broadly oval, short-stalked.

Altho sterile, our plants are identical with sterile forms of *L. hatcheri* (*L. baueriana*) of Schiffner in having 3-4 lobes to the leaves, the same cell measurements, thick cell walls and evident trigones.

On logs, soil or rocks in damp places. Yakima County (Brandegee), 1883; Olympic Mountains (Frye), 1907; Republic (Foster), 1912, 1913; Mt. Angeles near Port Angeles (Frye), 1927.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

Wyoming: Yellowstone Lake in Yellowstone National Park (Frye), 1925; Bears Den near Yellowstone Falls (Frye), 1925.

12. *Lophozia floerkei* (Weber & Mohr) Schiffner.

Plants bright green or brownish, caespitose or creeping; stems 5-30 mm long, creeping or ascending at apex, simple, sparingly branched or 2-3-forked; rhizoids colorless, long, numerous; leaves subimbricate, obliquely inserted, quadrate-rotund, .9-1.5 mm long, .7-1 mm wide; concave, divided $1/6-1/4$ their length into 3-5 unequal lobes, commonly 3-lobed; sinuses obtuse, spreading; lobes ovate, their apices acute and reflexed; margins undulate, with 1-2 ciliated teeth at base; underleaves present thruout, bifid to below middle, their lobes ciliate and .5-.7 mm long; leaf cells round-hexagonal, median ones 18-27 μ , thin-walled; trigones large and distinct; cuticle verruculose; gemmae wanting; dioicous; archegonia terminal; bracts subtransversely inserted, appressed, 4-5-lobed; lobes acuminate; bracteoles similar to underleaves, larger, bifid; perianth subcylindric, long-exserted, upper part plicate; mouth ciliate-dentate; androecium terminal; bracts 5-7 pairs, similar to stem leaves; antheridia 2-3; capsule brown, borne on a long stalk.

On wet soil. Stevens Pass in Cascade Mountains (Sandberg and Leiberg), 1893; Guemes Island (Frye), 1905; Elwha River valley in Olympic Mountains (Frye), 1907; Mt. Angeles (Foster), 1911; Lake Kechelus (Frye), 1921.

Montana: Holzinger Basin, Sperry Glacier region, (40).

13. *Lophozia attenuata* (Martius) Dumortier.

Plants in green or brown caespitose mats; stems 5-10 mm long, copiously branched, with numerous subfloral innovations; rhizoids numerous, long, colorless; leaves approximate to imbricate at apex, alternate, obliquely inserted, appressed or spreading, quadrate, .4-.5 mm long, divided $1/3-1/2$ their length into 2-4 subequal lobes; sinuses obtuse or sometimes acute, spreading; lobes triangular-ovate, acute

at apex; margin entire thruout; leaf cells 18-20 μ , round to hexagonal; walls thick; trigones small, distinct; cuticle striate; underleaves none; gemmae as golden-brown bunches at apices of upper leaves of flagella-like branches, numerous, irregular in shape, 2-celled; dioicous; archegonia terminal on main stem; bracts larger than leaves, 3-4-lobed, spreading; perianth 2/3 included, cylindric, plicate in upper part; mouth ciliate-dentate; antheridia unknown; capsule (according to Limpricht) nearly round, dark-brown; spores and elaters bright brown.

Roell reports finding it at Easton in 1888, (45).

Montana: Swiftcurrent Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

14. *Lophozia barbata* (Schmidel) Dumortier.

Plants bright or dark green or sometimes tinged with brown, in loose mats or thick tufts; stems either appressed on substrata and apices ascending, or ascending or erect thruout, 1-4 cm long, simple; rhizoids forming a thick felt, long, colorless; leaves approximate to imbricate, alternate, very obliquely inserted, spreading or ascending, broad at base, so inserted that the ventral basal margin is toward the stem apex, quadrate, 1-1.6 mm long, 1-1.4 mm wide, divided $\frac{1}{4}$ their length into 3-4 lobes; sinuses obtuse; lobes triangular-ovate, unequal, obtuse or acute; margin entire, free from appendages; underleaves present, oblong or quadrate, bifid nearly to base; their segments variously ciliated or toothed; leaf cells polygonal, not differing in basal portion, 15-36 μ ; walls thin; trigones small, inconspicuous; cuticle granulate; gemmae very rare, borne on delicate plants, not on flagelliform shoots, as golden brown clusters at apex of leaf lobes or on margin, 3-5-angled, 1-2-celled; dioicous; archegonia terminal; bracts similar to leaves, several pairs, 4-lobed; sinuses and lobes acute; margin at base with 1 or more teeth; innermost pair appressed to perianth; bracteoles larger than underleaves, more deeply segmented, connate with bracts or free. Androecium terminal or median, on slender plants; bracts 5-10 pairs, similar to leaves, rarely with 1-2 slender teeth at basal margin, concave; antheridia 2-5, with paraphyses; capsule long-ovate; spores brown, roughened with wart-like papillae.

North slope of Natatorium Park in Spokane (Bonser), 1907.

Montana: Lake McDonald, Sperry Glacier region, (40).

15. *Lophozia obtusa* (Lindberg) Evans.

Plants green or yellowish green, in loose tufts or mixed with

mosses; stems 2-5 cm long, thick, flexuous, ascending to erect, simple, with subfloral innovations, under surface reddish purple; rhizoids reddish purple at base, short, dense, numerous, to apex of stem; leaves remote to imbricate, horizontal to suberect, flaccid, upper part reflexed, rotund, slightly decurrent, bilobed to $\frac{1}{3}$ their length; sinus narrow, obtuse or rounded, gibbose and recurved at base; lobes ovate, rounded at apex, somewhat unequal, ventral the larger; cells 20-30 μ , oblong to round, 4-6-angled; walls thin; trigones small; cuticle striate-verruculose; underleaves triangular-subulate at forking of stem, wanting or rudimentary; gemmae at end of leaf lobes, pale green, angular, 1-celled; dioicous; bracts erect or partly reflexed, same size as leaves or smaller, margins often slightly dentate, irregularly 2-4-lobed, sinus obtuse or subacute, lobes acute, rarely obtuse; bracteoles large, variable, sometimes bilobed; perianth long exserted, narrowly cylindrical to cylindrical-clavate, smooth, plicate in upper part; mouth contracted, dentate-ciliate; antheridial bracts near middle of stem, 6-10 pairs, smaller than leaves, transverse, saccate, unequally lobed; lobes obtuse, incurved; antheridia 2-3, spherical.

On rocks. Friday Harbor (Daugherty), 1923; north side of Orcas Island (Clark), 1925.

Oregon: Portland (8).

SPHENOLOBUS

Plants green or brown, in caespitose mats or creeping among mosses; stems delicate, with subfloral or lateral branches, with or without stolons, ascending or erect or prostrate; rhizoids few or numerous, arising from base of leaves; leaves succubous or transversely inserted, embracing half the stem, remote or imbricate, suberect, ovate to obovate, or quadrate-rotund, concave, complicate, never with an acute keel, divided to $\frac{1}{7}$ - $\frac{1}{2}$ their length into 2 lobes; sinuses obtuse or acute, erect or spreading; lobes broadly triangular-ovate; apices obtuse or acute, converging; underleaves none or small and fugaceous; leaf cells small; dioicous or monoicous; archegonia terminal or falsely ventral; bracts several pairs, similar to leaves, imbricate or distinct, 2-3-lobed; bracteoles wanting or if present similar to leaves, 2-3-lobed; lobes equal or unequal; perianth exserted, ovate or obovate or cylindric, upper part plicate; mouth lobed, ciliate-dentate; spores and elaters brown.

A. Leaf lobes about equal, separated by an angular sinus.

B. Plants 1.5 mm wide; dorsal leaf lobe concave; involucre bracts embracing the perianth; perianth strongly plicate.

1. *S. minutus*

BB. Plants 2-3 mm wide; dorsal leaf lobe not concave; involucre bracts spreading almost at right angles to the stem; perianth plicate only at mouth.

2. *S. michauxii*

AA. Leaf lobes quite unequal, the dorsal not larger than one of the 2 teeth of the ventral, separated by a crescentic sinus.

3. *S. exsectus*

Species compared with *Jamesoniella*, *Gymnocolea* and *Lophozia* on page 76.

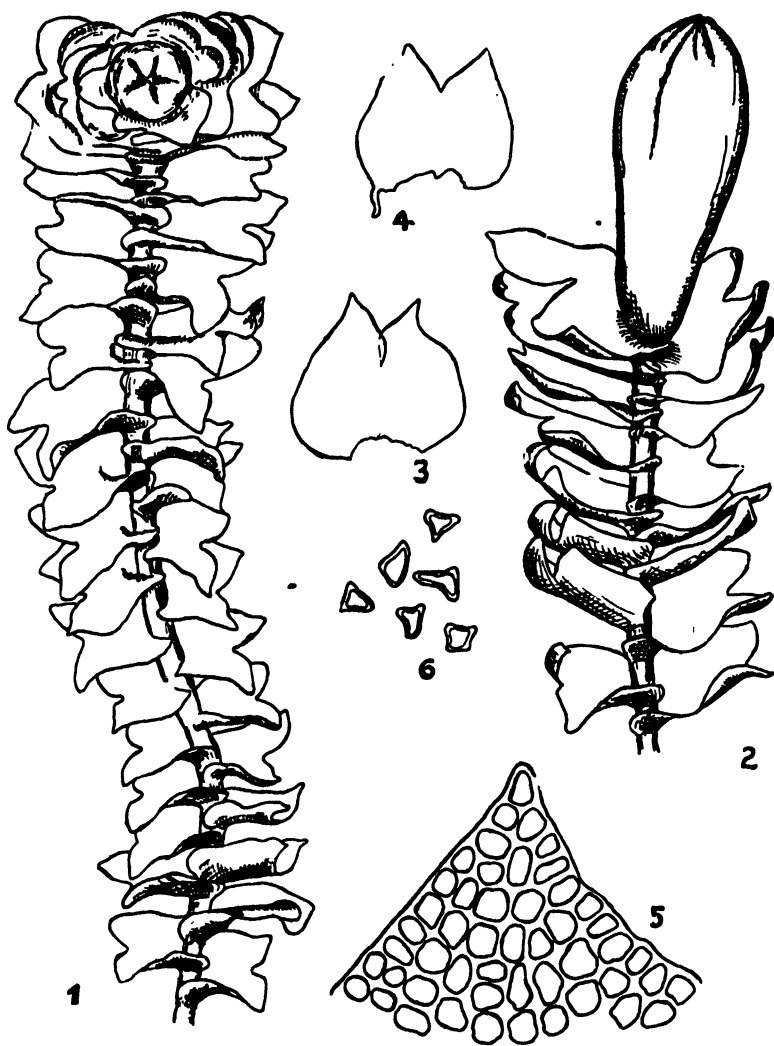
1. *Sphenolobus minutus* (Crantz) Stephani.

Plants bright green or brownish, in dense caespitose mats; stems 2-10 mm long, delicate, prostrate or ascending, simple to abundantly branched; rhizoids wanting or very scarce; leaves distant to imbricate, transversely inserted, subcomplicate, embracing half the stem, small, rotund, 4-5 mm long, divided for $\frac{1}{4}$ - $\frac{1}{3}$ their length into 2 equal or unequal lobes; sinus acute or obtuse, spreading; lobes acute, apices converging; leaf cells small 12-18 μ , sometimes at base 21-24 μ ; walls uniformly thickened; trigones none or indistinct; cuticle indistinctly roughened; gemmae dark yellow, variable in size and form, 2-celled, forming red bunches on leaf lobes; underleaves none; dioicous; archegonia terminal on main stem; bracts much larger than leaves, inner ones 3-4-lobed; perianth rotund, exserted for the most part, upper portion with 5 obtuse folds; mouth with 5 ciliate-dentate converging lobes; antheridia median on stem or on short innovations, solitary, large, oval, short-stalked; bracts similar to leaves, 4-12 pairs, complicate at base; capsule oval; wall bistratose; wall of outer layer with firm dark-brown thickenings; inner wall with imperfect semianular thickenings; spores densely papillose, tetrahedral, brown, 8-12 μ ; elaters with 2 spirals, brown.

On wet rocks. Stevens Pass in Cascade Mountains (Sandberg and Leiberger), 1893; Queets River valley in Olympic Mountains (Frye), 1907.

2. *Sphenolobus michauxii* (Weber) Stephani.

Plants in thick mats, brownish green to green; stems creeping or ascending, simple or sparingly branched, subfloral innovations to 4 cm; rhizoids few; leaves imbricate, at apex appressed, bases embracing the stem, sometimes half way or much beyond, broadly ovate



Sphenolobus michauxi. 1. Plant with young perianth at tip, $\times 25$. 2. Tip with mature perianth, $\times 25$. 3. Leaf, $\times 25$. 4. Male bract, $\times 25$. 5. Leaf cells, $\times 300$. 6. Gemmae, $\times 300$. (After K. Mueller).

to quadrate, bilobed to $\frac{1}{3}$ - $\frac{1}{2}$ their length, not complicate or indistinctly so; sinus broad, obtuse; lobes equal, ovate, acute; margins undulate, reflexed; ventral lobe oblique, dorsal lobe nearly horizontal; cells small, 10-20 μ , walls yellowish brown; trigones large, sometimes confluent; cuticle delicately papillate; underleaves none; gemmae clustered on tips of leaves of sterile or of antheridial branches, reddish, 3-4-

angled, 1-2-celled, thick-walled; dioicous; bracts larger than the leaves, more or less spreading from the perianth, deeply bilobed, sometimes with an extra tooth; bracteoles smaller, lanceolate, or wanting; perianth terminal; appearing lateral thru subfloral innovations, long exserted, 3 mm long, ovate to clavate, smooth, plicate at mouth into 5-6 folds; mouth lobed, finely dentate.

On rotten wood.

Idaho: Craig Mountain (Clark), 1924.

Wyoming: Norris Geyser Basin in Yellowstone National Park (Frye), 1925.

3. *Sphenolobus exsectus* (Schmidel) Stephani.

Plants small, scattered among mosses or in small compact yellowish green to light-brown patches; stems ascending, 5-30 mm long, more or less branched, brown to nearly black beneath, with innovations from below the female inflorescence; rhizoids numerous, long, colorless to brownish; leaves transversely inserted, not decurrent, imbricate or on the sterile stems somewhat distant, somewhat dorsally secund, the lower half erect-spreading, the upper half widely spreading to squarrose, concave, obliquely ovate or ovate-lanceolate, unequally and shortly bilobed; ventral margin large and strongly arched; dorsal margin shorter, less arched; dorsal lobe broadly subulate, almost reduced to a tooth; ventral lobe large, ovate, acute, frequently bidentate; sinuses crescentic; leaf cells 8-17 μ , rounded polygonal, the walls almost equally thickened; underleaves none; gemmae in reddish to yellowish clusters at the tips of the leaf lobes, elliptical, 2-celled, 12-17 μ by 9-11 μ ; dioicous; involucre bracts larger than the leaves, erect-spreading, round-quadrate, 3-5-lobed; lobes acute to acuminate, entire or dentate; perianth spinose-ciliate and spinose-dentate; male bracts in few pairs, imbricate, saccate at base, the dorsal lobe incurved; antheridia 1-2; capsule ovate, of 3 layers of cells, outer layer with knob-like thickenings, inner with semiannular thickenings; spores 9-12 μ ; elaters bispiral, reddish brown. (Adapted from MacVicar and K. Mueller).

This has been reported by Evans and Nichols from Colorado and Canada (9). It is therefore likely that it occurs in Montana and Wyoming. We know of no report of it from our area.

PLAGIOCHILA

Plants large; primary stem creeping, leafless or nearly so, rhizome-like, radiculose; secondary stem leafy, ascending or suberect, dark-

green or brownish, simple or dichotomous, sometimes pinnate and tree-like, without or with few rhizoids; leaves succubous, alternate, large, plane-distichous or deflexed, decurrent dorsally and more or less so ventrally, asymmetrical; apex round or truncate, dentate or spinose, rarely entire; dorsal margin straight or slightly concave, recurved at base, subentire; ventral margin plane or recurved at base, dentate or spinose, rarely entire; underleaves wanting except at apex, when present small or minute, entire, multifid or bifid irregularly cells medium to large; trigones distinct; archegonia terminal on leafy stem or branch; bracts distinct, free, similar to leaves, the large more strongly toothed; perianth exerted, strongly laterally compressed with more or less winged sutures dorsally or ventrally, companulate or obconic-cylindric; its mouth obliquely truncate, often bilobed; lobes dentate-spinose or ciliate; androecium terminal or medium, spicate; bracts smaller than leaves, closely imbricate, transversely inserted, erect at base, ventricose-saccate, basal margins adnate to stem; antheridia 1-10; calyptra free; capsule globose-oval, dehiscing by 4 straight valves; walls composed of several layers of cells, inner cells with numerous semiannular bands.

1. **Plagiochila asplenoides** (Linne) Dumortier.

Compared with *Leptoscyphus* and *Lophocolea* on page 95.

Plants pale or dark green, densely caespitose; secondary stem ascending to erect, 1-10 cm long, simple, dichotomous or sparingly branched laterally, with very few or no rhizoids; leaves alternate, subimbricate, orbicular-ovate or obovate-oblong, 1.5-2.5 mm broad, horizontal or erect-spreading; dorsal margin strongly reflexed, without teeth or cilia; ventral margin decurrent, subciliate or dentate; apex obtuse or rounded, subciliate or dentate or rarely entire; underleaves usually present at stem apex, small, subulate and entire or reduced to a ciliate cluster of cells; leaf cells hexagonal, 20-60 μ , thin-walled; trigones small, distinct; cuticle smooth; archegonial inflorescence terminal or falsely lateral by subfloral innovations; bracts not all different from stem leaves; perianth oblong, 3-5 mm long, often twisted in upper part, laterally compressed; its mouth bilabiate, denticulate; androecium terminal or median; bracts imbricate, transversely inserted, similar to leaves but saccate at base; antheridia 1-3, on stalks equal to their own length; capsule borne on a long stalk, 15-20 mm long; spores brown, 16-24 μ , minutely punctate.

On rocks or soil or wood in moist woods. Easton (Roell), 1888; Seattle (Piper), 1892; Snoqualmie (Piper), 1893; Cathlamet (Foster).

(?); Cascade Mountains (Allen), 1900; Paradise Valley on Mount Rainier (Flett), 1904; Hamilton (Foster), 1905; Ashford (Allen), 1905; Snoqualmie Falls (Frye), 1906; Elwha River in Olympic Mountains (Frye), 1907; South Bend (Frye), 1908; Westport (Foster), probably 1908; Mount Ellinor (Foster), 1911; Kalama (Frye), 1911; San Poil River (Foster), 1913; Sucia Islands (Daugherty), 1923; Friday Harbor (Daugherty), 1923; Speiden Island (Clark), 1925; Camas (Frye), 1925; Port Angeles (Frye), 1927; Mt. Angeles (Frye), 1927.

Oregon: Mt. Hood post office (30); Portland, Oregon City (31); Albany (Van Wert), about 1922; Santiam National Forest (Van Wert), about 1922.

Idaho: Farmington Landing (35); Moscow Mountain (Clark), 1923.

LEPTOSCYPHUS (Mylia)

Plants yellow or yellowish brown or dark green, forming thick mats or creeping among mosses; stems large, prostrate or ascending, simple or sparingly branched; rhizoids numerous, long, colorless; leaves succubous, alternate, imbricate, obliquely inserted, oval to sub-orbicular, erect or spreading, sometimes slightly decurrent; margin entire; apex rounded or emarginate; underleaves present thruout, lanceolate, entire; leaf cells large, round or hexagonal, those of gemmae-bearing plants elongated and the walls of the elongated cells often thickened with peg-like points; trigones present thruout, large, triangular or suborbicular; cuticle smooth or with reticulate papillae visible at leaf margin; dioicous; archegonia terminal on main stem, rarely on a branch, with 1 or more subfloral innovations; bracts similar to leaves; perianth free, cylindric at base, laterally compressed in upper part, not plicate; its mouth 2-lobed, dentate; capsule broadly elliptic.

1. *Leptoscyphus anomalus* (Hooker) Lindberg.

Compared with *Plagiochila* and *Lophocolea* on page 95.

Plants brown or yellowish brown or very rarely green, creeping or with mosses other than peat moss, sometimes erect; stem robust, prostrate with ascending apex or erect, 1-3 cm long, simple, very rarely branched; rhizoids numerous, long, colorless; leaves obliquely inserted, imbricate to closely imbricate at apex, obovate to orbicular, 1.12-2.5 mm long, .7-1.5 mm wide, subhorizontal or ascending, the concave apex rounded or rarely retuse or emarginate; margin entire, slightly reflexed; underleaves lanceolate, often of good size, obtuse, rarely emarginate or bilobed; leaf cells round to hexagonal, large, 45-60 μ , basal ones elongated, marginal ones quadrate; walls often

thickened with peg-like projections; trigones very large, triangular; cuticle smooth; gemmae abundant, borne in clusters at apex of elongated oval cells, large, greenish, oval or elliptic, 2-celled; dioicous; archegonial inflorescence terminal on main stem; bracts entire, similar to leaves but larger; perianth cylindric, compressed laterally, of a single layer of cells except at extreme base, its mouth entire or slightly undulate; androecium wanting in our specimens.

In peat bogs. Enumclaw (Roell), 1888; Mud Lake near Seattle (Piper), 1892; Hamilton (Foster), 1905; Copalis Rocks (Foster), 1911; Ronald (Frye), 1915; Mount Constitution (Wentworth), 1923.

LOPHOCOLEA

Plants yellowish green, pallescent, in thin spreading mats, large or rarely small, soft and flaccid; stems prostrate, subsimple or irregularly branched; branches lateral or latero-ventral; sexual branches often arising ventrally; rhizoids long, colorless, in tufts at base of underleaves; leaves succubous, alternate, very obliquely inserted, obliquely oblong-ovate, often nearly triangular or subquadrate, dorsally decurrent; apex truncate, usually bidentate or bifid; sinuses subacute to subrotund; margin entire; underleaves present thruout, cuneiform. ovate to subquadrate in outline, in our species the deeply bifid diverging segments again bifid; leaf cells mediumly large, thin-walled, occasionally with small trigones; dioicous or monoicous; archegonial inflorescence terminal on main stem or elongated branches, numerous; bracts larger than leaves, more deeply bifid or bidentate; perianth exserted, triangular-prismatic, third angle always dorsal, 2-4 times longer than broad, 3-lobed, bifid, ciliate-dentate or spinose, rarely entire or truncate; androecium terminal or median on branch; bracts several pairs, smaller than leaves, erect, imbricate, incurved, base saccate and lobate; antheridia solitary, large; capsule ellipsoid-oval, dehiscing to base by 4 straight rigid valves; walls many cells thick, outer layer with columnar or semiannular thickenings, inner layer thin, inmost layer with semiannular bands; seta long; elaters with 2 spirals.

A. Leaves 2-toothed or 2-lobed thruout.

B. Plant simple or once dichotomous; leaf cells 21-45 μ ;
spores 15-18 μ .

1. *L. bidentata*

BB. Plants many times branched.

C. Plants whitish; leaf cells 24-45 μ ; spores 16-17 μ ; mon-
oicous.

2. *L. cuspidata*

CC. Plants yellowish; leaf cells 20-30 μ ; spores 9-11 μ ;
heteroicous or dioicous.

4. *L. minor*

AA. Leaves 2-toothed below only; paroicous.

3. *L. heterophylla*

Comparison of species of <i>Plagiochila</i> , <i>Leptoscyphus</i> and <i>Lophocolea</i>	<i>Plagiochila</i> <i>asplenoides</i> p. 92	<i>Leptoscyphus</i> <i>anomalus</i> p. 93	Lophocolea			
			1. <i>bidentata</i>	2. <i>crispata</i>	3. <i>heterophylla</i>	4. <i>minor</i>
Underleaves present thruout or at tip only	t	p	p	p	p	p
Mouth of perianth unlobed, 2-lobed or 3-lobed	u	2	3	3	3	3
Trigones bulging into cells, or small to none	s	b	s	s	s	s
Perianth 3-angled, terete or laterally compressed	t	l	3	3	3	3
Leaf cells in mu	20-60	45-60	21-45	24-45	25-30	20-30
Spores in mu	12-16	15-18	15-18	16-17	11-13	9-11
Leaves 2-toothed thruout or below only			t	t	b	t
Dioicous, heteroicous, parioicous, monoicous	d	d	d	m	p	d-h
Plants whitish green, yellowish green, green, dark green, brownish green	g-d	b-y	w	w	w	y
Plants usually simple, once branched or more branched	1-m	s	s-o	m	o-m	o-m
Proportional depth to which leaf is notched	0	0	.1-.3	.2-.3	0-.3	.2-.4
Leaves entire, semiferous-erose, many-toothed, 2-lobed, bidentate	e-t	e-g	b	b	e-2	b-g
Underleaves entire, mere ciliate clusters of cells, or bifid to what proportion of their length	e-c	e-2	.5-.7	.5-.7	.5-.7	.7-.9
Length of plants in mm	10-100	10-40	5-15	6-20	6-20	5-15
Elaters yellowish brown, reddish brown, purple	p	r	r	r	y	r

1. *Lophocolea bidentata* (Linne) Dumortier.

Plants green or yellowish green, in densely caespitose mats; stems prostrate or ascending, dichotomous or laterally branched, 5-15 mm long; rhizoids numerous, long, colorless; leaves obliquely inserted, parallel to stem, alternate, almost oblong-ovate to subrotund, .7-.9 mm long, the same wide, gradually narrowing toward apex, divided to 1/8-1/4 their length into sharp teeth; sinuses broad, obtuse; lobes triangular-ovate to subulate-acuminate, unequal to subequal; underleaves subquadrate in general outline, deeply bifid with subulate diverging lobes; leaf cells hexagonal, 21-45 μ , thin-walled; trigones small but distinct; dioicous; archegonial inflorescence terminal but appearing as a lateral branch because of subfloral innovation; bracts close-

ly imbricate, transversely inserted, larger than leaves, obovate, deeply bifid; their margins entire or sparingly dentate; perianth exserted, triangular-prismatic; androecium terminal, in same tufts with archegonia; bracts smaller than leaves, closely imbricate, 4-6 pairs, unequally 2-3-lobed; at base toothed, saccate, with incurved toothed lobe; antheridia solitary; capsule oval, 2-5 layers of cells thick.

On moist earth. Easton (Roell), 1888; Seattle (Frye), 1904; Pacific Beach (Foster), 1911; Duwamish (Foster), 1911; Copalis (Foster), 1911; Burlington (Clark), 1913; Friday Harbor (Clark), 1925; Mt. Angeles near Port Angeles (Frye), 1927. Common about Seattle.

Idaho: Hope (2); Moscow Mountain (Clark), 1923.

2. *Lophocolea cuspidata* (Nees) Limpricht.

Plants green or pale green, in closely caespitose or repent-spreading mats; stems 6-20 mm long; branches lateral, occasionally dichotomous, prostrate or ascending at apex; rhizoids scarce, long and colorless; leaves obliquely inserted, imbricate, ovate to obovate-oblong, .7-1.5 mm long, .45-1.3 mm wide, equally or subequally narrowed toward the apex, bidentate for $\frac{1}{4}$ - $\frac{1}{3}$ their length; sinuses broad either crescentic or narrow and subobtusate; lobes long, subulate-acuminate, subequal, parallel or divergent; underleaves spreading, bifid; lobes unidentate at margin, or diverging and bifid; cells hexagonal, 24-45 μ ; walls thin; trigones small and distinct or wanting; cuticle smooth; monoicous; archegonial inflorescence on elongated lateral or latero-ventral branch 2-10 mm long; bracts closely imbricate, erect, canaliculate-concave, bifid to $\frac{1}{3}$ - $\frac{1}{2}$ their length; margin entire; bracteoles similar to the bracts in size and appearance; perianth exserted, triangular-prismatic, 2-3.5 mm long, 3-lobed for $\frac{1}{4}$ - $\frac{1}{2}$ its length; the lobes bifid; antheridial inflorescence terminal, rarely median; bracts imbricate, smaller, less acutely lobed than leaves, saccate dorsally; margin inflexed, with 1-2 teeth or lobes; antheridia solitary, subglobose; their stalks short, of 1 row of cells; capsule dark brown, 1-1.5 mm long; spores 15-21 μ , minutely punctate; elaters contorted, .15-.2 mm long, 9-12 μ wide in widest part.

On rotting sticks or logs or stumps, in moist woods. Roy (Allen), 1901; Seattle (Frye), 1904; Cathlamet (Foster), 1907; Westport (Foster), 1908; Friday Harbor (Clark), 1925; Olga (Peterson), 1925.

Oregon: Portland (31); Silverton (Foster), 1910; Albany (Van Wert), 1923.

Idaho: Moscow Mountain (Clark), 1923.

Montana: Polson (Frye), 1928.

3. *Lophocolea heterophylla* (Schrader) Dumortier.

Plants in pale green patches; stems to 2 cm, prostrate, irregularly branched; rhizoids numerous, in clusters; leaves more or less horizontal, oblong-quadrate, lower smaller, distant or approximate, bilobed; sinus obtuse; lobes obtuse or acute; upper leaves larger, imbricate; margin shortly decurrent; apex narrowed, rounded, truncate, retuse or broadly emarginate, rarely all leaves bilobed; cells 25-30 μ , polygonal; walls thin; trigones small; cuticle smooth; underleaves large, bifid to below middle, lobes subulate, acuminate, with a tooth or cilium near base; paroicous, rarely dioicous; bracts erect, larger than leaves, oblong-cuneate to oblong-quadrate, retuse or shortly and irregularly 2-4 lobed; bracteole deeply bifid; segments lanceolate margin with 1-3 cilia or teeth; perianth terminal on short branch, long exserted, cylindrical, sharply 3-angled above; mouth 3-lobed, dentate; capsule oval; spores 11-13 μ , yellowish brown, smooth; elaters reddish brown; antheridial bracts 3-5 pairs, more or less erect, similar to upper leaves, with dorsal lobe an inflated lobule.

On decaying wood. Ronald (Clark), 1924; Friday Harbor (Mullen), 1925; Olga (Clark), 1925.

Idaho: Moscow Mountain (Clark), 1923.

Montana: Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928; Polson (Frye), 1928.

Wyoming: Craig's Pass in Yellowstone National Park (Frye), 1925.

4. *Lophocolea minor* Nees, Naturg. Europ. Leberm. 2:330. 1836.

Jungermannia crocata De Notaris, Mem. Acad. Torino II. 1:323. 1839.

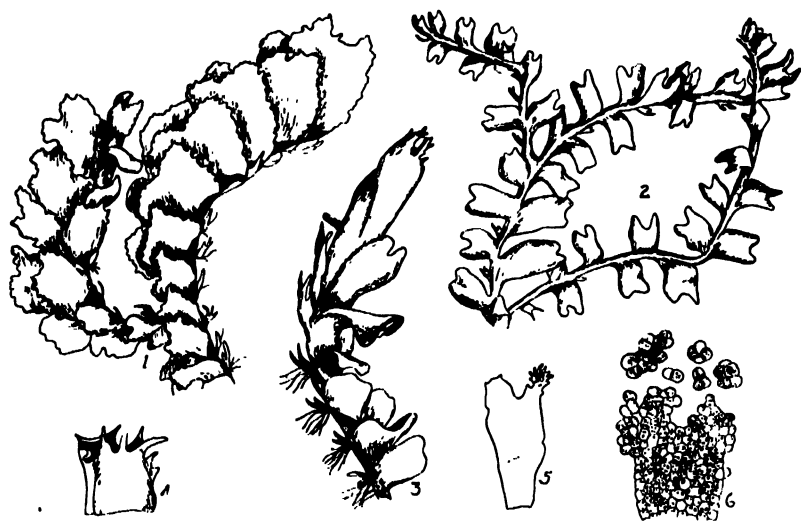
Lophocolea crocata Nees, Syn. Hep. p. 160. 1845.

Lophocolea heterophylla minor Douin, Rev. Bryologique, p. 23. 1907.

Plants prostrate, yellowish green, 1-2 mm wide, 5-15 mm long; stems green, somewhat laterally and often ventrally branched; rhizoids in tufts at the bases of the underleaves; leaves often too distant to overlap, succubous, almost longitudinally inserted, broadly ovate to almost quadrate, widest at their middle, bilobed for $\frac{1}{4}$ - $\frac{1}{3}$ their length; sinus acute to crescentic; lobes blunt, their margins entire or erose-gemmiferous; leaf cells 20-30 μ , thin-walled; trigones none or minute; underleaves bilobed almost to base, the lobes lanceolate, often with a tooth on the outer margin; gemmae almost always abundant,

not on underleaves, yellowish green, at first 1-celled and roundish, later forming masses or threads; dioicous, or sometimes paroicous; female bracts 2-3-lobed, larger than the leaves, rectangular; perianth small, elongated, sharply 3-angled above, the mouth with 3 large toothed lobes; male plants usually in separate tufts, their bracts sacate at base thru an upturned fold; antheridia solitary; spores about 10 μ , smooth; elaters bispiral, reddish.

Idaho: Craig Mountain (Clark), May 5, 1924.



Lophocolea minor. 1. Female plant with gemmae at margin of leaves, $\times 7.5$. 2. Sterile plant, $\times 12$. 3. Female plant with gemmae at mouth of perianth, $\times 7.5$. 4. Mouth of perianth, \times about 15. 5. Bract, $\times 7.5$. 6. Formation of gemmae from leaf, $\times 10$. (1, 2, 6, after Janzen; 3-5, after K. Mueller).

CHIOSCYPHUS

Plants yellowish green to black, densely caespitose or repent-spreading; stems 1-10 cm long, creeping, with numerous lateral or latero-ventral branches; rhizoids in tufts at base of underleaves, conspicuous, colorless, sometimes almost wanting, short; leaves succubous, alternate, distant, approximate or closely imbricate, very obliquely inserted, dorsally decurrent, spreading horizontally in the same plane, oblong or quadrate, concave ventrally; margin entire or dentate; apex ascending or suberect, rounded to acute; underleaves present thruout, cuneiform, ovate or subulate in general outline, deeply 2-4-lobed; leaf cells rather large, thin-walled, trigones indistinct or wanting; cuticle nearly smooth; dioicous or paroicous; archegonial in-

florescence on very short ventral or latero-ventral branch; bracts 1-2 pairs, outer pair minute, inner ones smaller than leaves; perianth usually campanulate or obconical, 3-angled at the 3-lobed mouth; androecium median or terminal; bracts much like leaves, with dorsal pouch; antheridia single or in twos; capsule oval, dehiscing to base by 4 straight valves; walls of 4-5 layers of cells; calyptra carnosose in lower part, shorter than perianth to much exserted; elaters with 2 spirals.

A. Leaf cells 21-50 μ ; perianth lobes entire or spinose-dentate.

B. Underleaves bilobed but not bifid; perianth lobes entire.

C. Plants terrestrial, green; cells 28-33 μ . 1. *C. polyanthus*

CC. Plants aquatic on stones and sticks, blackish green to dark green; cells 21-50 μ . 1a. var. *rivularis*

BB. Underleaves bifid; perianth lobes spinose-ciliate; plants dull green, slightly if at all transparent; cells 30-40 μ .

1b. var. *fragilis*

AA. Leaf cells 35-65 μ ; perianth lobes spinose-dentate, the perianth transparent; plants pale green; leaves entire to bilobed. 2. *C. pallescens*

Comparison of the species of Chiloscyphus, Geocalyx and Harpanthus	Chiloscyphus				Geocalyx gravolens p. 108	Harpanthus flotowianus p. 102
	1. <i>polyanthus</i>	1b. <i>p. fragilis</i>	1a. <i>p. rivularis</i>	2. <i>pallescens</i>		
Underleaves deeply bilobed, or entire to slightly toothed.....	b	b	b	b	b	c
Autoicous, dioicous.....	a	a	a	a	a	d
Perianth none, unlobed, 3-lobed.....	3	3	3	3	n	u
Cuticle smooth, finely punctate.....	s	s	s	s	p	s
Archegonia ventral, lateral.....	l	l	l	l	v	v
Leaf cells markedly transparent.....	—	—	—	+	—	—
Leaves commonly with some notching...	—	—	—	+	+	+
Plants not or usually in running water..	n	n	u	n	n	n
Plants green, blackish, brownish, dark, olive, yellowish.....	br-g	g-y	bl-d	g-y	y-o	y-b
Mouth of perianth or its lobes crenu- late, spinose, dentate, ciliate, entire... but commonly.....	c-sl c	sl s	c e	sd sl	× ×	c c
Proportional depth to which leaves are notched.....	0-1 1-5	0-1 1-8	0-1 1-10	0-2 1-3	.3-.4 .5-2	.05-.1 2-8
Length of plants in cm.....	28-33	30-40	21-50	35-65	21-48	28-36

1. **Chiloscyphus polyanthus** (Linne) Corda.

Plants green, on drying nearly black, in laxly caespitose or thickly intermingled mats; stems prostrate or ascending, 1-3 cm long, branches few; rhizoids numerous or nearly obsolete; leaves approximate to imbricate, horizontal, spreading, at apex ascending or sub-erect, quadrate-orbicular to oblong, .7-1.6 mm long, .54-1.2 mm wide, slightly concave ventrally; apex round to retuse; underleaves oblong-ovate, bifid to middle or below; their segments often linear-subulate, sometimes bearing a single tooth or cilium externally; leaf cells hexagonal, 15-33 μ , translucent; walls thin; trigones obscure or none; cuticle granulate or nearly smooth; autoicous; archegonial inflorescence terminal on a very short branch; bracts 1 pair, sometimes also a rudimentary second or outer pair, smaller than the leaves, bifid, sometimes retuse; bracteoles minutely bifid; perianth ovoid or goblet-shaped, 2-2.5 mm long, .9-1.5 mm wide, 3-lobed; its lobes truncate, entire, rarely dentate; androecium median or terminal on main stem; bracts similar to stem leaves, with small dorsal pouch, usually margined with soft cilia; antheridia single or occasionally in pairs; capsule brown, oval, 1.2-1.5 mm long; valves rigid, of 4-5 layers of cells; external layer thick, with columnar or imperfect semiannular thickenings; inner layer with semiannular bands; spores 14-20 μ , minutely granulate; elaters .12-.2 mm long, 8-11 μ wide.

The varieties of *C. polyanthus* grade into the type. Altho the variety *rivularis* has by some been raised to the dignity of a species, one wonders what changes would occur if it were removed from its water habitat and grown in damp air. Cultivation experiments with the members of this genus might prove to be highly enlightening concerning their relationship.

On logs and moist ground among mosses. Mason County (Piper), 1890; Mt. Rainier (Allen), 1900; Olga (Frye), 1904; Longmire Springs at base of Mt. Rainier (Frye), 1904; Nerada Falls on Mt. Rainier (Frye), 1904; Ashford (Allen), 1905; Calispell valley in Stevens County (Bonser), 1905; Olympic Mountains (Frye), 1907; Mt. Rainier (Foster), 1909; Burlington (Clark), 1910; Coweman River (Frye), 1911; Renton (Foster), 1912; Olympic Hot Springs (Foster), 1914; Lake Kechelus (Frye), 1921; Camas (Frye), 1925; Mt. Angeles (Frye), 1927. x

Oregon: Mt. Hood (45); McMinnville (Van Wert), about 1923.

Idaho: Rathdrum (45); Trude (Frye), 1925; Bonners Ferry (Frye), 1928.

Montana: Deer Lodge (45); Polson (Frye), 1928; Libby (Frye), 1928.

Wyoming: Yellowstone National Park (45), and (Frye), 1925; Centennial Hills and La Plata Mine in Albany County (42).

1a. Var. **rivularis** (Schrader) Nees.

Plants aquatic, larger in all parts than the typical plant, dark green to nearly black, sometimes with a fatty lustre; stems 1-10 cm long, abundantly branched, rhizoids scarce; leaves distant to imbricate, nearly flat and horizontal, orbicular, somewhat broader than long, 1.5-2.5 mm; apex rounded, rarely emarginate; cells 21-50 μ , opaque, walls thin; trigones wanting; underleaves destroyed or wanting except on young stems, shortly bilobed, segments subulate to filiform, margins entire; monoicous; so far our plants have been sterile.

In running water, on margins of streams. Hamilton (Foster), 1904; Aberdeen (Foster), probably 1908; Friday Harbor (Hartge), 1923; Sucia Islands (Clark), 1925; Olga (Clark), 1925; north side of Orcas Island (Osborn), 1925. Common about Seattle. The following collections by Roell in 1888 and referred by Stephani to *C. polyanthus* probably belong here: Tacoma, Easton, Rigi on Cle Elum Lake, Weston.

Oregon: Hult (Foster), 1910; Latourelle Falls (31).

Idaho: Moscow Mountain (Clark), 1923.

Montana: Holzinger Basin, Lake McDonald, Sperry Glacier, (40); Libby (Frye), 1928.

1b. Var. **fragilis** (Roth) K. Mueller.

Plants in springs or on wet ground, in dull green tufts; rhizoids scarce; leaves very large and flaccid, distinctly concave, broadly oblong-quadrate to roundish-quadrate; apex rounded, rarely slightly emarginate; cells large, 30-40 μ or more; walls thin; trigones none or minute; underleaves small, bifid, frequently destroyed; perianth with spinose-ciliate teeth on its lobes; calyptra long-exserted; spores 18 μ , yellowish brown; elaters 9 μ thick, bispiral.

Tacoma (Evans, Rhodora 14:217-218. 1912); north side Orcas Island (Clark), 1924.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928; Libby (Frye), 1928.

2. **Chiloscyphus pallescens** (Ehrhart) Dumortier.

Plants pale yellow or yellowish green, closely caespitose; stems prostrate or ascending, 1-3 cm long, sparingly to abundantly branched;

rhizoids conspicuous; leaves few, distant, ascending, distinctly convex, oblong- to roundish-quadrate, larger than in *C. polyanthus*, very frequently truncate; those near base of stem and on branches often rectangular, bilobed; lobes acute or obtuse; leaf cells hexagonal, 35-65 μ , with many golden-yellow chloroplasts; walls thin; trigones minute; underleaves large, oblong-ovate, spreading, bifid to middle or below; segments linear-subulate, tapering to a point, often bearing each a short segment or a cilium; autoicous; perianth 3-lobed, the lobes spinose dentate; calyptra equalling or exceeding the perianth, long exserted; spores 13-17 μ , yellowish brown, finely granulate; elaters 8-9 μ thick, reddish brown, bispiral.

Evans (Rhodora, 1905, p. 54) refers *C. adscendens* (Hooker & Wilson) Sullivant to *C. pallescens* as a synonym. K. Mueller (Rabenhorst's Kryptogamen-Flora 6:829. 1900-1911) does not agree with him. The reasons in so far as Mueller states them clearly are not convincing.

On logs in more or less dry places. Calispell valley in Stevens County (Bonser), 1905; Suiattle basin in Glacier Peak region (Winona Bailey), 1910; Olympic Hot Springs (Foster), 1914; Chico (Frye), 1915; Sucia Islands (Daugherty), 1923; Mt. Angeles (Frye), 1927; White River valley in Rainier National Park (Elizabeth Frye), 1928.

Oregon: Portland (44) as *C. adscendens*.

Idaho: Moscow Mountain (Clark), 1923; Bonners Ferry (Frye), 1928.

HARPANTHUS

Stems slender, slightly branched, the branches nearly always ventral; leaves succubous, alternate, emarginate or shortly bilobed; underleaves large, triangular-lanceolate, usually entire or with a tooth at the side, sometimes partly bifid, frequently connate at base on one side with the leaves; archegonia on short ventral branches; bracts very small, 2-3-lobed, bracteole resembling underleaves; perianth oblong, narrowed toward mouth, connate with calyptra for $\frac{2}{3}$ its length, several layers thick at lower part; calyptra free only near the apex; capsule oval, long stalked, wall bistratose, inner layer with semiannular thickenings; antheridia on short ventral branches.

1. *Harpanthus flotowianus* Nees.

Compared with *Geocalyx* and *Chiloscyphus* on page 99.

Plants green to yellowish brown, in large tufts or mixed with mosses; stems erect or ascending, slender and rigid, simple or with few

ventral branches; rhizoids colorless, numerous, short; leaves approximate to imbricate, flaccid, obliquely inserted, round-ovate to triangular-ovate, retuse or shortly emarginate, sinus small and lunate, lobes unequal and obtuse, dorsal margin strongly decurrent, ascending and somewhat secund; cells 28-36 μ , 5-6-angled, hyaline; walls thin; trigones small; cuticle smooth; underleaves large, erect-spreading, apex incurved, ovate-lanceolate, entire, sometimes with an obtuse tooth at side, sometimes bifid near base of stem; dioicous; archegonia on short ventral branches, inflorescence bud-like; bracts small, concave, 2-3-lobed; lobes acute or with incurved cilia, or obtuse; bracteole ovate-lanceolate; perianth cylindrical-clavate, curved, apex triplicate, mouth crenulate; capsule oval, brown; spores 9-12 μ , brown; antheridial branch geminate, short, ventral; bracts in 2-5 pairs, small, complicate-bilobed, concave, with dorsal tooth at base, lobes acute, apex incurved; antheridia 1-2, oval.

Sides of streams, wet banks and moist places. Ronald near Seattle (Clark), 1924.

Montana: Holzinger Basin, Sperry Glacier region, (40).

GEOCALYX

Plants similar to *Lophocolea* and *Chiloscyphus* in habit; stems prostrate, simple or sparingly branched; branches arising ventrally from axils of underleaves; rhizoids few or abundant, arising in tufts from base of underleaves; leaves succubous, alternate, bilobed or bidentate, slightly decurrent dorsally; underleaves present thruout, smaller than the leaves, bilobed to below the middle, free or connate to bases of leaves on one side by a narrow isthmus; archegonial inflorescences few, terminal on a very short branch arising from axil of an underleaf, the branch becoming a fleshy pendulose subterranean sac enclosing the young sporophyte and bearing at its mouth a few scale-like bracts which are destroyed on emersion of capsule; perianth wanting; androecium on a short ventral branch; bracts smaller than leaves, unequally and acuminate bilobed, sometimes with an additional tooth or lobule on dorsal margin; antheridia single, rarely in pairs, short-stalked; paraphyses none; calyptra shorter than perigynial tube, attached to it for 2/3 its length; archegonia at base of free portion; capsule cylindric, dehiscing to base by 4 straight valves; walls bistratose; outer layer with indistinct columnar or nodular thickenings; inner layer with semiannular bands; seta moderately long; elaters with 2 spirals. We have only the following species.

1. **Geocalyx graveolens** (Schrader) Nees.

Compared with Harpanthus and Chiloscypus on page 99.

Bright or olive green, densely caespitose, often intermingled with mosses; stems 5-20 mm long, prostrate, simple or with a few branches; leaves approximate or imbricate, very obliquely inserted in one plane on either side of the stem or suberect, rigid, ovate or quadrate-ovate, .8-1.5 mm long, .5-.7 mm wide, bilobed to 1/6-1/4 their length; lobes acute or subobtuse, connivent or parallel; sinuses very variable, rounded or acute; underleaves present thruout, appressed, bifid to below middle; their lobes lanceolate, nearly parallel; their sinuses acute or rounded; leaf-cells round to subquadrate, 21-48 μ ; chloroplasts numerous, arranged in a circle leaving a clear central space and a hyaline border next to the wall; basal and marginal cells not differing in shape from median; walls thin; trigones small; cuticle finely striate; autoicous; archegonial inflorescence terminal on short branch, becoming a subterranean perigynial tube, 2.5-3 mm long, 1 mm wide, radiculose most of its length; androecium terminal on a short branch, .3-1.2 mm long; capsule exerted, cylindric, dehiscing by 4 straight valves, 1-1.6 mm long; seta .08-.2 mm broad; spores 11-16 μ , granulate-papillate.

On rotten logs. Seattle (Piper), 1891; Olympia (Henderson), 1891; Whatcom Falls (Romine), 1907; Oysterville (Frye), 1908.

Idaho: Moscow Mountain (Clark), 1923.

CEPHALOSIELLA

Plants small or minute; stems without flagella, branches ventral, rarely lateral; leaves slightly or hardly broader than stem, almost transversely inserted, divided to the middle or deeper into 2 entire or rarely dentate lobes; cells usually small; archegonial inflorescence terminal on main stem; bracts larger than the leaves, in 3 rows, more or less connate at the base, dentate, rarely entire; perianth usually elongated and narrow, 3-6-plicate; the mouth constricted, truncate, crenulate or dentate; seta usually composed of 4 large external cells in cross section, with a few small central cells which are often not apparent.

A. Leaf lobes entire; cell walls comparatively thin.

B. Underleaves wanting on the sterile branches; autoicous or parocious.

C. Usually parocious; cells 16-20 μ long; elaters 6-7 μ thick.

3. *C. limprichtii*

CC. Autoicous; cells 11-18 μ long; elaters 8-9 μ thick.

2. *C. hampeana*

BB. Underleaves present on sterile stems; dioicous. 1. *C. starkei*

AA. Leaf lobes crenulate or dentate; cell walls comparatively thick.

D. Leaf lobes 4-8 cells wide at base; underleaves present on sterile as well as reproductive branches.

E. Leaf notch distinctly less than a right angle; leaves papillose; stems 3-10 mm long; underleaves usually bilobed.

1a. var. *scabra*

EE. Leaf notch about a right angle; leaf surface verruculose; stems .5-1.5 mm long; underleaves usually not bilobed.

4. *C. alpina*

DD. Leaf lobes 12-14 cells wide at base; underleaves wanting on sterile and reproductive stems.

5. *C. turneri*

Comparison of species of Cephaloziella	3. <i>limprichtii</i>	2. <i>hampeana</i>	1. <i>starkei</i>	1b. <i>starkei</i> <i>scabra</i>	4. <i>alpina</i>	5. <i>turneri</i>
Except for bilobing, leaves of sterile stems entire, crenulate, dentate.....	c	c	c	d	cd	d
Cell walls comparatively thin.....	+	+	+	-	-	-
Female bracts how many times as large as leaves.....	4-5	3-5	5-8	4-6	3-5	2-3
Monoicous, paroicous, autoicous, dioicous.....	pa	a	d	d	m	md
Length of cells in mu.....	18-20	11-18	10-15	8-12	10-20	12-18
Diameter of elaters in mu.....	6-7	8-9	6-8	6-8	10	8
Number of cells in basal width of leaf lobe.....	5-7	4-8	6-10	7-8	4-7	12-14
Underleaves usually bilobed.....	-	-	-	+	-	X
Cuticle smooth, verruculose, papillose...	s	s	s	p	v	s
Leaf notch about a right angle, or distinctly less.....	a	a	a	l	a	l
Length of stems in mm.....	5-10	3-10	3-10	3-10	.5-1.5	2-5
Rhizoids usually few or many.....	f	f	f-m	f-m	m	m
Underleaves on sterile or reproductive branches, or on neither.....	sr	n	sr	sr	sr	n
Spores in mu.....	8-12	8-9	7-9	5-6	10-14	8

1. *Cephaloziella starkei* (Funck) Schiffner.

Cephaloziella divaricata Dumortier, Hep. Eur. p. 89. 1874.

Plants small, green or olive green or black, often tinged with red, creeping among mosses, caespitose; stems prostrate to ascending,

stout for the size of the plant, 7-8 cells in diameter, 1-10 mm long, sparingly branched; cortical and inner cells not differing; rhizoids numerous, short, colorless; leaves distant to imbricate, transversely inserted, ascending, small, suborbicular-quadrate or subquadrate, .084-.21 mm long, .08-.2 mm wide, bifid to below the middle; lobes sub-complicate, triangular-ovate, acute or subobtuse or rarely subacuminate, divergent, entire or repand or with a small tooth; underleaves distinct on both sterile and fertile stems, lanceolate-subulate with apex incurved; leaf cells small, nearly quadrate, 10-16 μ , opaque or clear; walls thick or thin; trigones present; cuticle smooth or granulate; gemmae in yellowish green to reddish clusters at apex of sterile stems; dioicous; archegonial inflorescence terminal on main stem; bracts 3 pairs, 2-3 times as large as the leaves, bilobed or rarely trilobed; dorsal lobe free or connate with the bracteoles; lobes acute, dentate, subspinulose or nearly entire, margin hyaline at apex; bracteoles similar to the bracts, outer 2 smaller, less deeply bifid than the bracts; perianth fusiform-ovate to linear, .08-.14 mm long, .2-.4 mm wide, 3-6-angled, hyaline toward apex, purplish below, slightly constricted at mouth; mouth denticulate or subentire; walls unistratose; androecium terminal or median on main stem or branch; bracts several pairs, concave, imbricate, more acutely lobed than the leaves; capsule oval, spores yellowish brown, almost smooth; elaters broad, bispiral.

On logs and charred stumps, with mosses and other hepatics. University campus at Seattle (Piper), 1891; Ilwaco (Frye), 1908; Aberdeen (Foster), 1908; Pacific Beach (Foster), 1910; Copalis Crossing (Foster), 1911.

Wyoming: Norris Geyser Basin in Yellowstone National Park (Frye), 1925.

1a. Var. **scabra** (Howe), new comb.

Cephaloziella asperifolia C. Jensen, Medd. om Groenland 15:371. 1879. Not
Jungermannia asperifolia Taylor, Jour. of Bot. 1846: 277. 1846 (=

Cephalozia asperifolia Stephani, Spec. Hep. 3:338. 1908).

Cephalozia divaricata scabra Howe, Mem. Torrey Bot. Club 7:129. 1899.

Cephalozia papillosa Douin, Rev. Bryologique 28:72. 1901.

Cephaloziella papillosa Schiffner, Oester. Bot. Zeit. 1905:55. 1905.

Cephaloziella douini Schiffner, Oester. Bot. Zeit. 1905:55. 1905.

Cephaloziella asprella Stephani, Spec. Hep. 3:337. 1908.

Cephaloziella byssacea asperifolia MacVicar, Handbook Brit. Hep., 1st. Ed., p. 275. 1912.

Cephaloziella starkei asperifolia MacVicar, Handbook Brit. Hep., 2nd. Ed., 1926.

Plants dark green or brownish; stems rarely with paraphyllia-like appendages; leaves distant, spreading to erect-spreading, about

twice as wide as the stem, slightly broader than long, bilobed for $\frac{1}{3}$ - $\frac{1}{2}$ their length, often 2-3 cells thick at base; lobes lanceolate, acute, 7-8 cells wide at base, the tip 1 cell wide for 1-3 cells, the margin dentate; cuticle distinctly papillose, the dorsal with some large papillae composed of 1 or more cells; leaf cells round-quadrate, 8-12 μ ; underleaves oval to lanceolate, usually bilobed; gemmae spherical to ovoid, mostly 1-celled, green, 9-11 μ long; dioicous; bracts of the female inflorescence larger than the leaves, not connate, usually much less papillose than the leaves; perianth about $\frac{2}{3}$ exserted, deeply 3-6-plicate, 2 cells thick at base; mouth somewhat contracted, crenulate; bracts of the male inflorescence strongly concave, spinose-dentate, without the large surface papillae of the leaves; spores 5-6 μ , smooth.

On logs in deep woods. Mt. Constitution (Frye), 1904; Hamilton (Foster), 1905; Gate (Foster), 1912.

Oregon: Rainier (31); Portland (31).

2. *Cephaloziella hampeana* (Nees) Schiffner.

Plants in reddish brown, sometimes green patches; stems 3-10 mm long, prostrate, rigid, sparingly branched, with subfloral innovations; rhizoids long, colorless; leaves distant, erect-spreading, oblong, cuneate, on sterile stems as broad as stem or slightly broader, bilobed to below middle; lobes 5-8 cells broad at base, rarely 4, lanceolate, acute, divergent; sinus acute; leaves on fertile stems imbricate, erect-spreading to erect, roundish quadrate, bilobed to half their length; lobes acute, entire; cells 14-18 μ , more or less quadrate; walls often strongly and equally thickened; cuticle smooth or nearly so; underleaves absent, rare on apex of sterile stems; autoicous; archegonia terminal on stem or elongated branch; bracts larger than leaves, bilobed to $\frac{1}{3}$ their length; lobes acute, crenulate-dentate to dentate, rarely entire, apex sometimes hyaline; bracteole smaller than leaves, adnate to bracts at base, bilobed, lobes crenulate to denticulate; perianth oblong, 3-6-plicate, reddish brown below, hyaline above, mouth crenulate-dentate with elongated cells; antheridia terminal on long branches; bracts 6-10 pairs, larger than leaves, imbricate, very concave, bilobed to $\frac{1}{3}$ their length; lobes apiculate or acute, entire.

Pacific Beach (Foster), 1911.

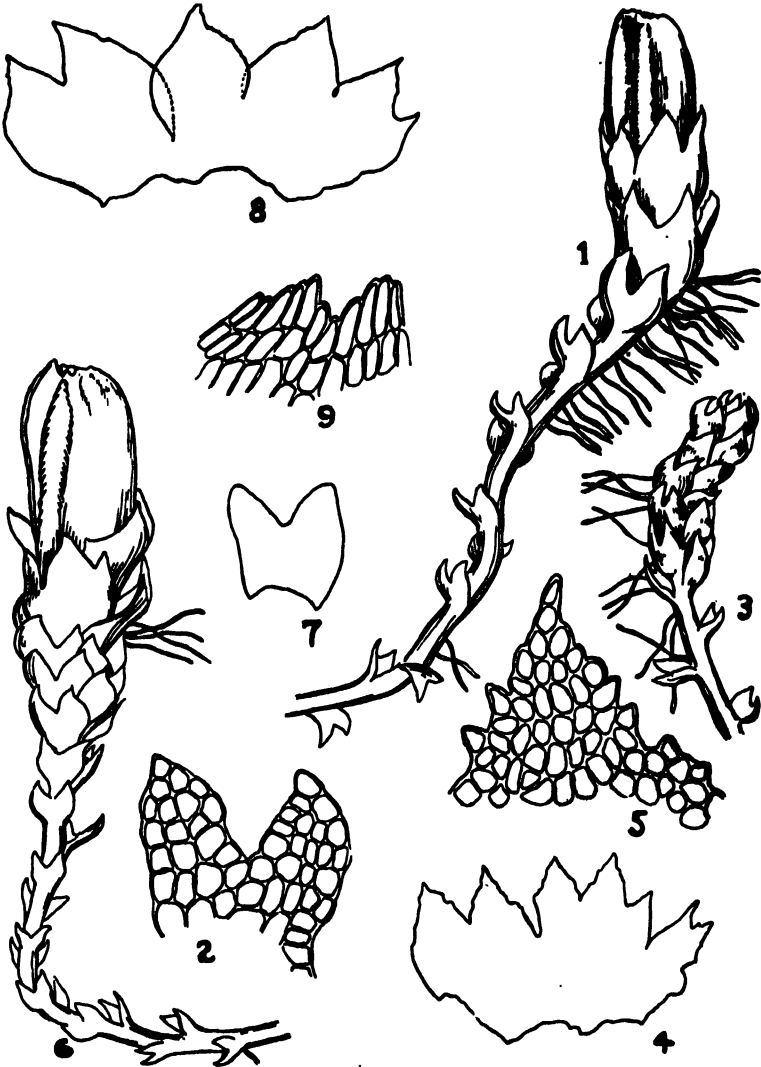
3. *Cephaloziella limprichtii* Warnstorf, Krypt. Fl. d. Mark Brandenburg 1:228. 1902.

Cephalozia stellulifera gracillima Douin, in Bull. Soc. Bot. France 52:259. 1905.

Cephaloziella gracillima Douin, in Mem. Soc. Nat. Sci. Cherbourg 25:257. 1906.

Cephalosiella stellulifera limprichtii MacVicar, Student's Handbook Brit. Hep.
2nd edition, p. 289. 1926.

In thin yellowish green patches, becoming dark with age; stems up to 10 mm long, prostrate, simple or with subfloral innovations; rhizoids rather scarce; leaves distant to subimbricate, erect or as-



Cephalosiella limprichtii. 1. Plant with perianth, $\times 50$. 2. Leaf cells, $\times 210$. 3. Male branch, $\times 50$. 4. United female bracts, $\times 50$. 5. Tip of female bract, $\times 210$. 6. Plant with perianth, $\times 50$. 7. Leaf, $\times 70$. 8. United female bracts, $\times 50$. 9. Portion of perianth mouth, $\times 210$. (After K. Mueller).

ceding, divided to about the middle into oblong-quadrate or narrowly ovate-lanceolate lobes, apex frequently incurved; lobes 5-7 cells wide at base, acute; leaf cells 16-20 μ , rectangular or quadrate; walls slightly and equally thickened; cuticle finely punctate; underleaves distinct on both sterile and fertile stems, erect, subulate, rarely bifid; gemmae on the margins of the uppermost leaves and underleaves, green, roundish-oval, 1-2-celled; parocious or sometimes monoicous; female inflorescence at tip of branch or stem; bracts imbricate, concave, larger than the leaves, bilobed to $\frac{1}{3}$ their length; lobes acute, entire, connate with each other and with the bracteoles; sinus acute; perianth narrowly oblong, $\frac{1}{2}$ exserted, 3-6-plicate, the mouth hyaline and crenulate with elongated and projecting cells; capsule cylindrical-oblong; spores reddish brown, finely papillose.

According to Dr. A. W. Evans this has been found in Washington, but we have seen no material from our area.

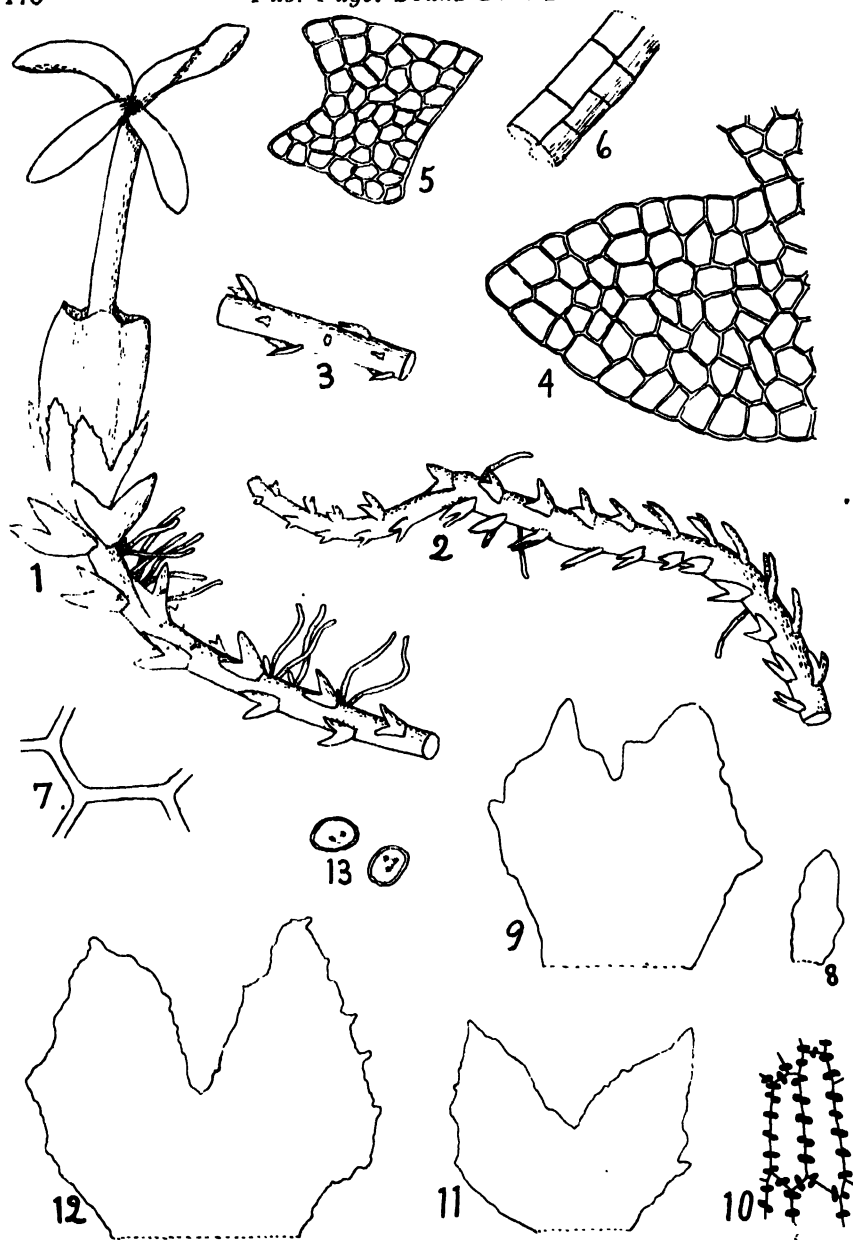
4. **Cephaloziella alpina** Douin,* Mem. Soc. Bot. France 29:70. 1920.

Plants in green patches, minute; stems prostrate, .5-1.5 mm long, apex ascending, simple or sparingly branched; rhizoids numerous, long, colorless or tinged with brown, extending nearly to the apex of the stem; leaves distant to imbricate at apex, erect-spreading, more or less quadrate, .09-.19 mm long, .14-.16 mm wide, bilobed for about $\frac{1}{2}$ their length; lobes 4-7 cells wide at base, acute; sinus acute or almost a right angle; margin distinctly crenulate; leaves at apex with a few irregular teeth; leaf cells more or less quadrate, 10-20 μ , walls strongly and equally thickened; cuticle minutely verruculose; underleaves present on the sterile stems as well as on the fertile ones, mostly simple, lanceolate or subulate, 50-70 μ long, 20-40 μ wide, very rarely bilobed; monoicous; inflorescence at apex of stem; bracts 2-3 pairs, .2 mm long, .24 mm wide, larger than the leaves, bilobed for about $\frac{1}{3}$ - $\frac{1}{2}$ their length; margin with small irregular teeth; perianth oblong, .49-.68 mm long, 4-plicate in upper part, green to hyaline below, more or less hyaline above; mouth crenulate with long teeth; capsule brown, .2 mm long; elaters brown, .05-.1 mm long, .01 mm wide, bispiral; spores brown, smooth, 10-14 μ .

On rotten logs.

Idaho: Genesee Ridge near Moscow (Clark), 1923.

*We are very short of literature, but thru the kindness of Dr. M. A. Howe of the New York Botanical Garden we can give two citations to Douin's own published articles, already with his own name after it. These are: (a) Revue Gen. Bot. 28:269, 1916; and Mem. Soc. Bot. France 29:70, 1916. The plant is described and figured from the material from Moscow Mountain, near Moscow, Idaho, and referred to this species by Dr. A. W. Evans, to whom also we are indebted for the original citation above.



Cephaloziella alpina. 1. Plant, semidiagrammatic, $\times 40$. 2. Flagellum, dorsal view, $\times 155$. 3. Part of flagellum, ventral view, $\times 155$. 4. Part of leaf, $\times 670$. 5. Leaf from flagellum, $\times 670$. 6. Part of stalk of capsule, semidiagrammatic, $\times 100$. 7. Cell angles, $\times 1400$. 8. Underleaf from sterile branch, $\times 155$. 9. Underleaf from near tip of fertile branch, $\times 155$. 10. Thickenings in capsule wall, inner view, $\times 670$. 11. Second bract, $\times 155$. 12. First bract, $\times 155$. 13. Spores, $\times 670$.

5. **Cephaloxiella turneri** (Hooker) K. Mueller.

Plants bright green or pallid or rusty brown, depressed-caespitose or creeping among mosses; stems round, .06-.1 mm in diameter, 2-6 mm long; branches lateral or latero-ventral or rarely strictly ventral, the cortical cells pellucid; rhizoids few; leaves approximately to closely imbricate and equitant, complicate-bilobed for $\frac{1}{2}$ - $\frac{2}{3}$ their length; lobes ovate to ovate-lanceolate, apiculate or acute; dorsal lobes suberect, broader; ventral lobes usually spreading; whole leaf margin sharply and unequally serrate-dentate; underleaves wanting thruout; leaf cells 14-20 μ ; walls thick; trigones present; dioicous; archegonial inflorescence terminal on elongated branch; bracts 2-3 pairs, increasing in size upwards; innermost larger than leaves, often connate with each other and bracteoles, dentate, bifid; lobes acute or subacuminate; bracteoles ovate, subacuminate, spinulose-dentate; outer bracts free, outer bracteoles wanting; perianth linear-oblong, 1-3-sided with pronounced ridges, unistratose or rarely bistratose at base of angles, often decolorate toward mouth; mouth nearly closed, denticulate; androecium median, perigonal leaves similar to stem leaves, a little larger, more closely imbricate; capsule oblong-ovate.

On slightly shaded soil. Mount Rainier (Piper), 1895.

CEPHALOZIA

Green or whitish or brown or dark green or sometimes tinged with red, small or medium or minute, depressed-caespitose or creeping among mosses; stems leafy or rhizomatous at base or bearing flagella, sparingly branched; branches arising ventrally; rhizoids numerous or few; leaves succubous, alternate, often nearly horizontal, obliquely or rarely subtransversely inserted, rather broad, more or less concave, bifid for $\frac{1}{3}$ - $\frac{1}{2}$ their length or more; apices sometimes connivent; margins plane or incurved, never recurved, entire; underleaves smaller than leaves and entire, or wanting except in association with bracts, equal to and similar to the bracts when with them, or wanting thruout; leaf cells rather large and pellucid; walls thick or specially thick at angles or thin; cuticle smooth or slightly roughened; gemmae present in a few species at stem-apex or on leaf-margins; archegonia several to numerous, terminal on short or elongated branches; bracts free from perianth, much larger than leaves, 3 rows of 3 pairs, 2-4-lobed, often dentate or incised; innermost bracteole always present, similar to the bracts, more or less connate to the bracts on 1 or both sides, outer bracteoles somewhat smaller; perianth more or less emersed, 2-7 times longer than broad, 3-angled at least when young,

1 angle ventral, upper part constricted, basal wall 1-3 cells thick; mouth denticulate, ciliate, lancinate; androecium median, rarely terminal or occupying an entire branch; bracts similar to the leaves, slightly larger or smaller, imbricate, more concave, sometimes with a small accessory incurved lobule on dorsal margin; antheridia solitary; calyptra small, thin, rarely fleshy surrounded at base by sterile archegonia; capsule long exserted, delicate, cylindric-oblong or oblong-globose, opening to base by 4 valves; walls bistratose, inner cells with semianular thickenings; stalk pellucid; elaters with 2 spirals, deciduous, subobtuse, mostly .15-.2 mm long, 8-10 μ wide; spores smooth or minutely roughened, 8-10 μ .

A. Leaves bilobed for $\frac{1}{2}$ their length or more; dorsal leaf-margin not decurrent; perianth 1 cell thick in the middle.

B. Leaf cells 30-60 μ ; plants monoicous.

C. Flagella common; leaves bilobed for $\frac{1}{2}$ - $\frac{2}{3}$ their length; female bracts notched for $\frac{2}{3}$ their length.

1. *C. bicuspidata*

CC. Flagella none or rare; leaves bilobed for about $\frac{1}{2}$ their length; female bracts notched for about $\frac{1}{2}$ their length.

1a. var. *lammersiana*

BB. Leaf cells 18-24 μ ; plants dioicous.

4. *C. leucantha*

AA. Leaves bilobed for about $\frac{1}{3}$ their length; dorsal leaf-margin usually decurrent; perianth 2-3 cells thick in the middle.

D. Flagella present; plants monoicous; tip of leaf lobe one cell thick for about 1 cell long.

2. *C. pleniceps*

DD. Flagella none; plants dioicous; tip of leaf lobe one cell thick for about 2 cells long.

3. *C. media*

Comparison of species of Cephalozia	1. <i>bicuspidata</i>	1a. <i>lammersiana</i>	2. <i>pleniceps</i>	3. <i>media</i>	4. <i>leucantha</i>
Length of cells in μ	30-60	35-42	30-45	30-60	18-24
Depth to which leaves are notched.....	$\frac{1}{2}$ - $\frac{2}{3}$	$\frac{1}{2}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{2}$
Number cells perianth is thick in middle.....	1	1	2	2-3	1
Depth to which female bracts are notched.....	$\frac{2}{3}$	$\frac{1}{2}$	$\frac{1}{4}$ - $\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{4}$ - $\frac{1}{3}$
Stems usually with flagella.....	+	-	+	-	-
Monoicous, dioicous.....	m	m	m	d	d
Usual number of single cells in tip of leaf lobe..	2	2	1	2	2
Dorsal leaf-margin decurrent.....	-	-	\pm	+	-
Leaves inserted nearly transversely or distinctly diagonal.....	d	d-t	d	d	t

1. **Cephalozia bicuspidata** (Linne) Dumortier.

Cephalozia extensa Spruce, On *Cephalozia*, p. 44. 1882.

Yellowish or bright green, depressed-caespitose; stem prostrate, round, sparingly branched, often with flagellae, round, 6-7 cells in diameter, its cortical cells large pellucid, its inner cells small; rhizoids long, numerous, colorless; leaves quadrate-oval or sometimes ovate, .15-.3 mm long (Howe says .3-.65 mm.), 12-.5 mm wide, obliquely or subtransversely inserted, distant to imbricate, bifid to $\frac{1}{2}$ - $\frac{3}{4}$ the leaf length, concave, subcomplicate; lobes triangular-lanceolate or triangular, connivent or erect, acuminate or the ventral lobe acute, dorsal lobe sometimes apiculate (2 cells); entire; sinuses obtuse; underleaves wanting except in association with archegonial bracts; leaf cells hexagonal to quadrate, elongated at base, 30-60 μ , pellucid; walls thin; trigones wanting or very minute; cuticle smooth; gemmae rare, whitish green, spherical, 1-celled, in clusters at apex of branches; dioicous; archegonial inflorescence terminal on very short or rarely elongated ventral branch; bracts 3 pairs, inner ones twice as large as the leaves, bifid to middle; lobes lanceolate-acuminate, entire or with 1 or more teeth near the base or repand; bracteoles similar; perianth fusiform or linear-fusiform, exerted 3 times the length of the bracts, 1.5-2.5 mm long, .3-.5 mm wide, 3-angled when young, becoming nearly cylindric in lower part; mouth constricted, denticulate; unistratose thruout; androecium terminal, median or occupying the entire branch; bracts similar to the leaves, more concave, imbricate, often with a small accessory tooth on dorsal lobe at base; calyptra thin; capsule oval or cylindric-oblong, brown or tinged with red, .6-.75 mm long, .3-.5 mm wide; spores purple.

On decaying logs or moist earth, with mosses. Seattle (Piper), 1891; Stevens Pass (Sandberg and Leiberg), 1893; Cascade Mountains (Allen), 1900; Mt. Rainier (Frye), 1904; Tacoma (Flett), 1905; Hamilton (Foster), 1905; Whatcom County (Romine), 1907; Olympic Mountains (Frye), 1907; Westport (Foster), 1908; Nahcotta (Frye), 1908; Ashford (Foster), 1909; Buck Creek in Glacier Peak region (Winona Bailey), 1910; Copalis Crossing (Foster), 1911; Olympic Hot Springs (Foster), 1914; Snoqualmie Pass (Frye), 1921; north side of Orcas Island (Clark), 1925; Friday Harbor (Clark), 1925; La Push (Frye), 1927.

Oregon: Mt. Hood (45); Powers Creek (Foster), 1910; Cape Arago (Frye), 1922.

Idaho: Moscow Mountain (Clark), 1923 .

Montana: Lake McDonald (40).

Wyoming: Yellowstone National Park (45); Norris Geyser Basin in Yellowstone National Park (Frye), 1925.

1a. Var. **lammersiana** (Huebener) Breidler.

Plants in rather compact tufts; flagella none or rare; leaves rather distant, distinctly concave, bilobed for $1/2$ - $2/3$ their length; their lobes unequal, incurved and somewhat connivent; monoicous or falsely dioicous; female inflorescence on elongate or rarely short ventral branches; involucre bracts entire or sinuate or with a tooth on one side, divided to below the middle.

Oregon: Portland (44).

We have not seen this material, and its inclusion rests upon Pearson's determination of the collection mentioned above.

2. **Cephalozia pleniceps** (Austin) Lindberg.

Plants green or tinged with brown, densely caespitose, sometimes erect and forming thick cushions; stems erect, 3-20 mm long, irregularly branched, 8 cells in diameter, flattened dorsally, its cortical cells large and pellucid; flagella present; rhizoids numerous, long, colorless; leaves subimbricate to distant, obliquely inserted, ascending, very concave, orbicular, .26-.5 mm in diameter, scarcely if at all decurrent, bifid to $1/3$ their length; sinuses obtuse or rarely acute; lobes lanceolate, acute or the ventral one subobtuse, connivent; underleaves rudimentary if present, at apex of young stem; leaf cells quadrate-hexagonal but becoming elongated at base, 30-60 μ ; walls thick, pellucid; monoicous; archegonial inflorescence terminal on a short branch; bracts 3 pairs, innermost ones 2-4-lobed, free or united with bracteoles; bracteoles similar to the leaves; lobes acute or lanceolate; perianth cylindric, 1.61-2.66 mm long, terete, 3 cell-layers thick at base, bistratose at middle and above, constricted; its mouth crenulate-dentate; antheridia terminal or median; bracts with incurved teeth or lobes at base; calyptra thin; spores brown, 12-18 μ , densely papillate.

On logs. Near Seattle (Bailey), 1905; Hamilton (Foster), 1905; Buck Creek in Glacier Peak Region (Winona Bailey), 1910; Burlington (Clark), 1910; Pacific Beach (Foster), 1911; north side of Orcas Island (Clark), 1925.

3. **Cephalozia media** Lindberg.

Plants bright or pale green, densely caespitose or creeping among mosses; stem 3-20 mm long, irregularly sparingly branched, somewhat flattened dorsally, ascending at apex, cortical cells large and

pellucid; flagella none; rhizoids numerous, long, colorless; leaves sub-imbricate and ascending or distant and subhorizontal, obliquely inserted, decurrent dorsally, orbicular to rhomboidal, .14-.4 mm in diameter, bifid to $\frac{1}{3}$ their length; sinuses obtuse or rounded; lobes triangular-ovate, acute or subacuminate, connivent; margin entire; underleaves none; leaf cells large, pale, 30-60 μ , walls thin; trigones none; dioicous; archegonial inflorescence terminal on short ventral branches; bracts 3-4 pairs, orbicular-oblong, bifid to below the middle, innermost larger than leaves; segments acute or acuminate; margin entire or sparingly denticulate; bracteoles similar, often united to bracts; perianth oblong-fusiform to linear, 2.5-3.5 mm long, constricted toward mouth, denticulate at mouth, of 2-3 layers of cells at base, bistratose at middle, the rest unistratose; antheridial inflorescence terminal on short branch, median or occupying all of the branch; bracts similar to leaves and more concave; antheridia in spikes; calyptra 2-3 cells thick thruout; capsule cylindric, .6-8 mm long, .2-.5 mm wide; spores light brown, 10-12 μ , minutely roughened.

On decaying logs in damp woods; common in western Washington. Seattle (Piper), 1891; Mount Rainier (Piper), 1895; Cascade Mountains (Allen), 1900; Seattle (Frye), 1904; Friday Harbor (Frye), 1904; Paradise River on Mount Rainier (Frye), 1904; Calispell River (Bonser), 1905; Exposition Gulch in Tacoma (Flett), 1905; Lacentre (Davis), year (?); Elwha River valley in Olympic Mountains (Frye), 1907; South Bend (Frye), 1908; Burlington (Clark), 1910; Kalama (Frye), 1911; Pacific Beach (Foster), 1911; Yacolt (Frye), 1911; Ronald near Seattle (Foster), 1911; Gate (Foster), 1912; Port Angeles (Foster), 1914; Olympic Hot Springs (Foster), 1914; North Bend (Frye), 1921; Sucia Islands (Clark), 1924; Orcas Island (Clark), 1924; junction of Greenwater and White Rivers (Frye), 1926; La Push (Frye), 1927. Here probably belongs the plant collected by Roell at Enumclaw in 1888 and referred by Stephani to *C. connivens*.

Oregon: Portland (44), and (Flinn) 1912; Cape Arago (Frye), 1922; Bandon (Frye), 1922.

Idaho: Moscow Mountain (Clark), 1923.

Montana: Lake McDonald, Sperry Glacier region, (41); Iceberg Lake trail from Many Glaciers in Glacier National Park (Frye), 1928; Polson (Frye), 1928; Whitefish (Frye), 1928; Libby (Frye), 1928.

Wyoming: Craigs Pass in Yellowstone National Park (Frye), 1925.

4. *Cephalozia leucantha* Spruce.

Plants pale green, depressed caespitose; stems prostrate, delicate, sparingly branched, 6 cells in diameter, outer cells large and pellucid, inner cells smaller; flagella none; rhizoids few, scattered, colorless; leaves distant to subimbricate at apex, nearly transversely or obliquely inserted, dorsal margin not decurrent, slightly spreading to erect, concave, ovate, .136-.2 mm long, .098-.13 mm wide, bifid to the middle or a little beyond; lobes triangular, connivent or spreading, acute or apiculate; sinuses obtuse or subacute; underleaves none; leaf cells oblong-quadrate, 18-24 μ ; walls uniformly thickened; dioicous; archegonial inflorescence on a very short branch; bracts 2-3 pairs, orbicular; inner pair bifid to $\frac{1}{3}$ their length; lobes spreading; sinuses obtuse; margin subentire very slightly denticulate; other bracts small, similar to the leaves whose margins are subentire; bracteoles triangularly bilobed, their lobes entire and obtuse; perianth ovate-cylindric, 1.4-2.8 mm long, .5 mm wide, terete, unistratose thruout, 3-4-keeled above, somewhat constricted at mouth; mouth irregularly lobed, the lobes denticulate or ciliate; androecium terminal on ventral branch, sometimes median on other branches; bracts 2-5 pairs, imbricate, strongly concave, bifid to $\frac{1}{3}$ their length; antheridia single; capsule purplish brown, on a long seta; spores yellowish brown, 9-12 μ , minutely verruculose; elaters with 2 spirals, .15-.25 mm long, 9 μ wide.

In Europe the leaf cells of this species seem to be smaller, 12-18 μ .

On decaying logs. Near Nahcotta (Frye), 1908.

HYGROBIELLA

Plants bright or dark green, densely caespitose; stems roundish, erect, leafy or flagellum-like, delicate, branches arising from ventral axis of leaf as lateral or subfloral innovations or as ventral flagella, often numerous branches at base of plant; rhizoids very few or wanting thruout; leaves slightly incubous or transversely inserted, erect, complicate-bilobed for $\frac{1}{3}$ their length, distant to subimbricate; margin entire; apex of lobes obtuse or acute; underleaves either nearly as large as stem-leaves and similar, or wanting thruout; segments equal or subequal; leaf cells large, often twice as long as wide; walls thin; trigones present; cuticle smooth; dioicous; archegonial inflorescence terminal on main stem or short branch; bracts 2-3 pairs, a little larger than but similar to the stem leaves; lobes subequal; perianth lanceolate-fusiform or elongated, bluntly 3-5-angled, con-

tracted at mouth; its mouth dentate; androecium terminal; bracts 5-7 pairs, imbricate, ovate, bifid, concave; antheridia large, single, often surrounded by leafy processes; capsules oblong, reddish brown, of 2 layers of cells; elaters with 2 spirals. We have only the following species.

1. ***Hygrobrella laxifolia*** (Hooker) Spruce.

Compared with *Pleuroclada*, *Odontoschisma* and *Calypogeia* on page 121.

Plants delicate, small, 5-15 mm long, with subfloral innovations, branches lateral or at base of stem; rhizoids wanting or very few; leaves transversely inserted, erect, complicate-bilobed, subimbricate to distant; margins entire; sinuses extending about $\frac{1}{3}$ leaf-length; apex of lobes obtuse or acute; leaf cells oblong or hexagonal, about twice as long as broad, 40-70 μ long, 20-30 μ wide; walls thin; trigones distinct; underleaves similar to leaves; dioicous; archegonial inflorescence terminal on main stem or short branch; bracts similar to leaves but less deeply bifid; lobes unequal, sheathing the base of the perianth; perianth lanceolate-fusiform when mature; its cells 3-4 times as long as broad; its mouth contracted, narrow, with 15 hyaline projecting cells; androecium terminal; bracts 5-7 pairs, imbricate; antheridia typical; calyptra $\frac{1}{2}$ as long as perianth; capsule reddish brown, bistratose; spores reddish, 20-24 μ ; elaters with 2 spirals, light brown, rather short.

The lateral branches, large underleaves and elongated cells separate this plant at once from *Cephalozia* and *Cephaloziella*; and there is little probability of confusing it with any other genera.

On wet rocks. Paradise Valley on Mt. Rainier (Frye), 1904 and (Foster), 1909.

Oregon: Hult (Foster), 1910.

Idaho: Hope (35).

PLEUROCLADA

Plants whitish or glaucescent; stems procumbent, pinnate or subpinnate, with rhizoids; branches all lateral, subtended by a 1-lobed leaf; leaves transversely inserted, bilobed, very concave; underleaves large, entire or 1-toothed; archegonia terminal; perianth fleshy, of several layers of cells at base, trigonous, contracted at the mouth; capsule oblong-cylindrical, wall of 2 layers of cells, inner layer of cells with semiannular thickenings. There is only the following species.

1. *Pleuroclada albescens* (Hooker) Spruce.

Compared with *Hygrobrella*, *Odontoschisma* and *Calypogeia* on page 121.

Plants in large loosely matted and depressed tufts, whitish green, becoming slightly bluish white in drying; stems up to 3 cm long but the American plants under 9 mm, procumbent, loosely subpinnate, branching 2 or 3 times dichotomously, slightly radiculose, with rhizoids up to apex; leaves somewhat distant, alternate, almost transversely inserted, slightly succubous, concave, almost hemispherical, bilobed for $\frac{1}{3}$ their length; segments ovate, triangular, connivent; sinus narrow or subobtusate; axillary leaf produced partly from stem and partly from the adnate branch; differs from the other leaves in being broadly ovate, subcordate at base, not bifid, apex acute; cells quadrate or hexagonal, smooth, pellucid, with delicate walls; trigones none; underleaves subcontiguous, appressed, plane, slightly shorter than the leaves, broadly ovate to ovate-lanceolate, acute or subacuminate, rarely obtuse, on one side above the base deeply unidentate, sometimes unidentate on both sides or entire; dioicous; perianth terminal on short or long branches which are radiculose at the base, much exserted, 8 times as large as the stem leaves, clavate or linear-fusiform, deeply trigonous, fleshy, 5-8 cells thick near the base; cells large, elongated, pellucid; mouth constricted, often scariose, afterwards lacerate and erose; bracts 3 pairs, appressed, convolute, the lower a little larger than the leaves, the upper almost 3 times larger, free or slightly connate at base, oblong-quadrate, bilobed to $\frac{1}{4}$ their length, rarely trifid, segments subacuminate or acute; bracteoles smaller, entire or bifid at apex, provided on both sides near the base with 1-3 large teeth; calyptra pyriform, delicate, of a purplish brown color like the spores and elaters.

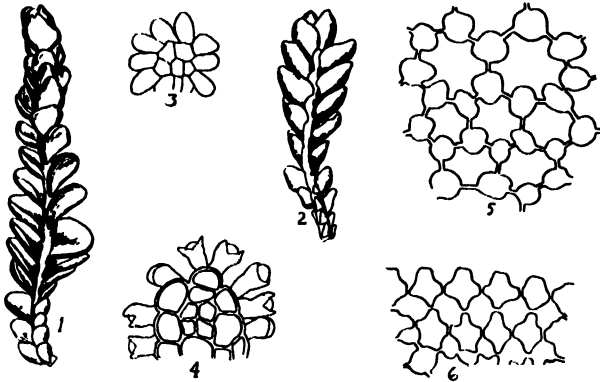
On damp earth in alpine localities. Mt. Rainier (32).

Montana: Sperry Glacier (32).

ODONTOSCHISMA

Plants rather large, in green or reddish or dark brown tufts; stem creeping, not from a rhizomatous base; rhizoids present; branches nearly always ventral; flagella present, always ventral; leaves succubous, obliquely or almost longitudinally inserted, somewhat concave, round or ovate, entire, rarely emarginate; cell walls thick; underleaves usually small or obsolete except among the bracts; female inflorescence cladogenous; bracts in 3 rows, usually bifid; perianth large, trigonous;

mouth contracted, dentate or ciliate or rarely nearly entire; calyptra thin; capsule oval.



Odontoschisma gibbsiae. 1. Part of plant with 3-ranked leaves above, $\times 9$. 2. Part of plant, ventral view, $\times 9$. 3. Median leaf cells, $\times 175$. 4. Marginal leaf cells, $\times 125$. 5. Young underleaf, $\times 125$. 6. More mature underleaf, $\times 125$. (After Evans).

1. ***Odontoschisma gibbsiae*** Evans, Bot. Gaz. 36:341. 1903.

Compared with *Hygrobella*, *Pleuroclada* and *Calypogeia* on page 121.

Plants yellowish green, more or less tinged with red or brown, growing in depressed mats or creeping among other bryophytes; stems sparingly and irregularly branched, .3 mm in diameter, prostrate, ascending at the tips; flagella ventral or terminating leafy branches; vegetative branches varying from ventral to lateral; rhizoids scanty; leaves imbricate, strongly concave, increasing in size from the base of a leafy axis, orbicular, 1 mm long, not bordered, attached by an oblique line of insertion, slightly decurrent dorsally, more or less dilated at ventral base, arching to or beyond the middle of the stem; margin entire; apex rounded; leaf cells about 16 by 23 μ at margin, the median ones about 19 μ , the basal about 23 μ ; trigones very large, rounded, occasionally confluent; cell cavities stellate, with distinct pits, pigmentation when present limited to the lining of the cavity; cuticle very thick, smooth or minutely verruculose; underleaves minute except at the base of a branch, irregular in form, sometimes vaguely bidentate; gemmiferous branches long, worm-like, simple, terminating normal vegetative branches, prostrate or ascending; their leaves in 3 equal rows, somewhat transversely inserted, imbricate, concave, oblong, variously erose-dentate at apex and upper margins; gemmae oval to pyriform, arising singly or in chains from the margin and outer

surface of the leaves and finally from the stem apex, 1-celled or usually 2-celled, with thick outer wall and thin transverse partition, occasionally mixed with slime-papillae; inflorescence and sporophyte unknown. (Adapted from Evans).

The only collection of this so far as we are aware, is that of the type at Port Renfrew on the south shore of Vancouver Island (20), but its occurrence on the adjacent Washington shore is highly probable.

CALYPOGEIA

Plants medium sized, light green or becoming dark on drying, depressed-caespitose; stems prostrate or ascending at apex, often bearing gemmae at apices, subsimple or irregularly branched; branches arising somewhat laterally from axil of underleaves, rhizoids long, colorless, numerous, in clusters at base of underleaves; leaves incubous, alternate, plane or convex, ovate or subrhomboidal, rounded or retuse or less commonly acute at apex, bidentate or bilobed; margin entire; underleaves present thruout, smaller than the leaves, suborbicular or reniform or ovate, bifid or retuse or rarely entire; leaf cells large, pellucid or with chlorophyll; trigones rarely present; sexual branches single or in pairs or sometimes in threes, arising from axils of underleaves; archegonial branch a fleshy cylindric subterranean pouch bearing numerous rhizoids; bracts 2-3 pairs, smaller than the stem leaves, suborbicular or ovate or lanceolate or entire or 2-4-lobed; archegonia 4-12; mouth of tube with scale-like bracts, lined within with clavate-papilliform cells; androecium small, capitate or linear; bracts small, bifid; calyptra adnate for $\frac{3}{4}$ of its length to perigynium, free portion surrounded by unfertilized archegonia; capsule cylindric, dehiscing to base by 4 spiral valves; walls bistratose, outer layer nearly destitute of local thickenings, inner layer with numerous semi-annular bands; seta long; elaters with 2 spirals.

A. Leaf cells 30-60 μ , the cell-hollow angular; underleaves approximately as wide as the stem.

B. Underleaves bilobed to less than their middle, the lobes blunt; spores 12-16 μ .

1. *C. trichomanis*

BB. Underleaves bilobed to their middle or beyond, the lobes acutely pointed; spores 9-11 μ .

2. *C. fissa*

AA. Leaf cells 21-36 μ , the cell-hollow roundish; underleaves approximately twice as wide as the stem.

3. *C. suecica*

Comparison of species of Hygrobrella, Pleuroclada, Odontoschisma and Calypogeia	Hygrobrella laxifolia, p. 116	Pleuroclada albescent. p. 117	Odontoschisma griffithiae, p. 118	Calypogeia		
				1. tricho- manis	2. fissa	3. succisa
Perianth present.....	+	+	+	-	-	-
Rhizoids clustered.....	-	-	-	+	+	+
Leaves succubously, transversely or incubously inserted.....	t	t	s	i	i	i
Proportional depth to which leaves are notched.....	.2-.5	.3-.4	0	0	0-.1	0.
Leaves entire, retuse, 2-lobed.....	2	e-r	c	c-2	r-2	c-2
Spores in mu.....	20-24	10-12		12-16	9-11	8-10
Cell-hollow roundish, angular.....	a	r	a	a	a	r
Cells in mu.....	28-63	24-30	16-23	30-60	40-55	21-36
Underleaves about how many times as wide as the stem.....	2-4	1	1	1	1	2
Underleaves unlobed, or the lobes blunt or pointed.....	u-p	u-p	u	b	p	p
Proportional depth to which under- leaves are notched.....	0-.3	0	0	.3-.4	.5-.7	.5-.6
Rhizoids abundant, scarce.....	s	s	a-s	a	a	a
Underleaves entire, 1-toothed, 2-toothed	e-2	e-1	c	2	2	2

1. *Calypogeia trichomanis* (Linne) Corda.

Plants light green, densely caespitose or mixed with mosses, stems 6-25 mm long, subsimple or sparingly branched, prostrate or ascending; rhizoids long, colorless, numerous; leaves approximate to distant or closely imbricate, .7-1.1 mm long, .6-1.4 mm in widest part, decurrent ventrally, acute or retuse or commonly rounded or more rarely bidentate; margin entire; underleaves orbicular or ovate, broader than the stem, distant or subimbricate, usually bifid to $\frac{1}{4}$ of their length or less but sometimes to below the middle, .2-35 mm long, .28-.42 mm wide; lobes obtuse; margin entire or rarely with a tooth on the outer side; sinus shallow and rounded; base more or less decurrent, attached by an arched line; leaf cells 30-60 μ , chloroplasts close to long axis of cell; wall thin; trigones none; gemmae ovoid, of 1-2 cells when present, in clusters on small leaves at stem tips; autoicous; perigynium tube 2.1-2.5 mm long, .6-.9 mm wide; archegonia 4-7; antheridial inflorescence short, capitate, attaining a length of nearly 1 mm, occurring in the axil with the archegonial branch; antheridia solitary, ovoid, short stalked; capsule 1-2 mm long; seta 1-2.5 mm long; spores 12-16 μ , minutely punctate; elaters obtuse, .18-.35 mm long, 11-15 μ wide.

On moist banks in woods; common in western Washington. Mt. Rainier (Piper), 1895; Cascade Mountains (Allen), 1900; Paradise Valley on Mt. Rainier (Frye), 1904; Seattle (Frye), 1905; Olympic Mountains (Frye), 1907; Ilwaco (Frye), 1908; Pacific Beach (Foster), 1911; Olympic Hot Springs (Foster), 1914; Friday Harbor (Daugherty), 1923; Olga (Clark), 1925; north side of Mt. Constitution (Millican), 1925; Mt. Angeles (Frye), 1927; Darrington (Frye), 1928.

Oregon: Powers Creek (Foster), 1910; Portland (Flinn), 1912.

Idaho: Moscow Mountain (Clark), 1923.

Wyoming: Norris Geyser Basin in Yellowstone National Park (Frye), 1925.

2. *Calypogeia fissa* (Linne) Raddi.

Plants translucent, bluish green, flat; stems 2-5 cm long, thin, fragile, prostrate or ascending, sparingly branched; rhizoids long, colorless, numerous, in tufts from the bases of the underleaves thruout the stem; leaves very obliquely inserted, incubous, about $\frac{1}{3}$ encircling the stem, spreading to horizontal, slightly convex, oblong-ovate to broadly ovate, 1.5-2 mm long, 1 mm wide, slightly or not decurrent; apex frequently decurved, narrowed, bidentate or at most bilobed to $\frac{1}{3}$ the leaf-length; teeth or lobes triangular-ovate, 3-5 cells wide at base to nearly wanting, sub-acute or obtuse; cells 40-55 μ , thin walled, hexagonal; trigones none or minute; cuticle smooth, or slightly rough near the base of the leaf; underleaves smaller than the leaves, usually much wider than long, commonly about 45-70 μ , more than twice as wide as the stem, distant, spreading, slightly or not decurrent, bilobed for $\frac{1}{2}$ - $\frac{2}{3}$ their length; lobes divaricate, obtuse or subacute, frequently with a broad lobe or obtuse tooth above the middle; sinus acute or obtuse; gemmae in subglobose clusters on the tips of small-leaved stems or branches, 1-2-celled, spherical to ellipsoidal, yellowish green; autoicous or paroicous, rarely dioicous; capsule cylindrical, brown, the walls of 2 layers of cells; inner layer with numerous reddish brown semiannular thickenings; spores 9-12 μ , smooth, pale brown; elaters 8-10 μ thick, bispiral, reddish brown.

Reported from Washington by C. M. Roberts and F. W. Grant.
Oregon: Portland (44).

3. *Calypogeia suecica* (Arnell and Persson) K. Mueller.

Plants light or yellowish green, depressed-caespitose; stems prostrate with ascending apex, subsimple or irregularly branched, 5-15

mm long; apices small-leaved and gemmiferous; rhizoids numerous, long, colorless; leaves distant to approximate, oblong to triangular-ovate, convex or at apex occasionally revolute, .4-.9 mm long, .4-.7 mm wide, spreading at an angle of 45° from stem, slightly decurrent ventrally; apices varying from rounded to bifid; sinuses and teeth acute to rounded; underleaves large, about .45 mm long, .45-.6 mm wide, remote to subimbricate at apex, broadly orbicular, bifid to the middle or beyond; lobes acute or obtuse; sinus angular or crescentic; margin entire or with 1-2 teeth; leaf cells 21-36 μ , hexagonal, outer cells with distinct trigones; cuticle smooth; gemmiferous stems numerous; gemmae globose or oblong, hyaline, 2-celled; dioicous; young perigynium tube 1.5-2 mm long, .9-1 mm wide; male inflorescence small, capitate; capsule 2-3 mm long, about .5 mm wide, cylindrical, pointed; its stalk 1 cm long, hyaline; inner wall with numerous parallel semiannular thickenings; outer wall of 8 rows of cells of which alternate ones contain knob-like thickenings; spores 8-10 μ , brown; elaters 8-10 μ thick, bispiral, reddish brown. (Sporophyte characters after K. Mueller).

On rotten logs in moist woods. Mt. Rainier (Frye), 1904; Tacoma (Flett), 1905; Olympic Mountains (Frye), 1907; Seattle (Clark), 1910; Kalama (Frye), 1911; Pacific Beach (Foster), 1911; Renton (Foster), 1911; Port Angeles (Foster), 1914.

BAZZANIA

Plants green or brownish green, loosely to densely caespitose; stems robust, ascending, often decurved, dichotomous, bearing numerous small-leaved flagella; leaves incubous, alternate, obliquely inserted, imbricate, plane or convex, ovate-triangular from a subcordate base, 3-4-toothed or rarely 2; apex decurved; margin entire; underleaves rotund-quadrate, 4-lobed or entire; leaf cells nearly round; trigones large, triangular; cuticle smooth; dioicous; archegonial inflorescence on a very short ventral branch; bracts smaller than the leaves but similar to them; perianth cylindric, 3-angled at base when young, later 3-6-angled at apex; mouth dentate or denticulate or entire; antheridial inflorescence terminal on a short ventral branch; bracts several pairs, similar to the stem leaves; capsule oval, long-exserted; spores brown, papillose; elaters with 2 spirals.

The genus needs revision, and species determinations should be considered tentative. Perhaps all the collections from the northwest should be referred to the same species.

- A. Underleaves about as wide as long; most of the underleaves entire or 2-toothed; leaves not enrolling the stem when dry; cuticle smooth. 1. *B. ambigua*
- AA. Underleaves wider than long; most of the underleaves 3-4-toothed; leaves enrolling the stem when dry; cuticle granulate. 2. *B. tricenata*

Comparison of species of <i>Bazzania</i> and <i>Lepidozia</i>	<i>Bazzania</i>		<i>Lepidozia</i> reptans p. 127
	1. <i>ambigua</i>	2. <i>tricenata</i>	
Leaves rather wider than long, or rather longer than wide.	l	l	w
Proportional depth to which leaves are notched.	0-.1	0-.2	.3-.5
Dioicous, autoicous.	d	d	a
Underleaves wider than long, or about the same each way.	s	w	w
Length of stems in mm.	15-20	30-80	5-60
Tips of leaves mostly entire, or emarginate, or how many toothed or lobed.	c-2	3-4	4
Leaf cells in mu.	20±	24-30	22-48
Leaves enrolling the stem when dry.	—	+	
Cuticle smooth, granulate.	s	g	s
Female bracts deeply or shallowly divided.	s	d	d
Spores in mu.	12-14	15-16	14-16

1. *Bazzania ambigua* (Lindenberg) Trevisan, in Mem, 1st Lomb. 13:414. 1845.

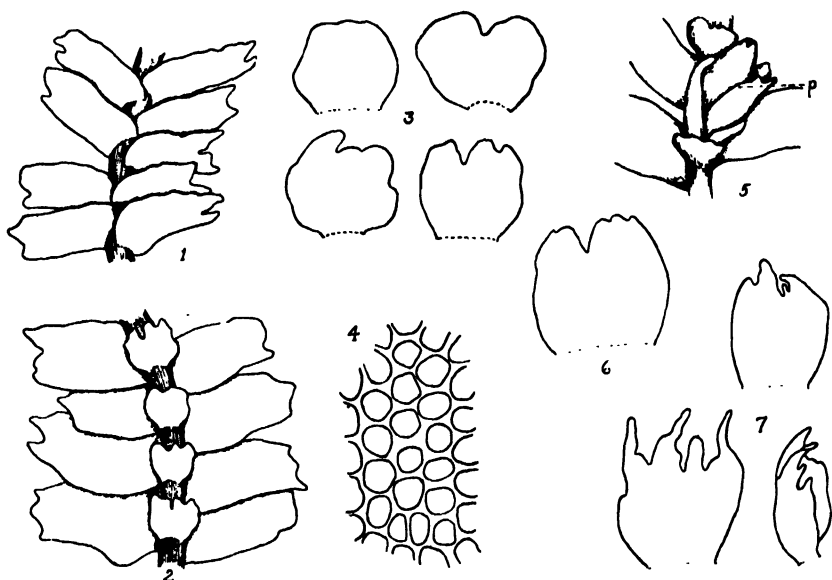
Mastigobryum ambiguum Lindenberg in part, G.L.N. Syn. Hep. p. 217. 1845.

Plants prostrate to suberect, 1.5-2 cm long, 1-2 mm wide; stems sparingly branched; rhizoids none or few; leaves contiguous to loosely imbricate, widely spreading but rarely at right angles, distinctly convex, slightly falcate, mostly ovate to oblong-ovate, usually .7-.9 mm long and .45-.6 mm wide, apex typically bidentate; sinus shallow, lunate or subacute; lobes subacute, the upper often a shade the larger; median leaf cells about 20 μ ; cuticle smooth; trigones small but distinct, with straight sides; underleaves slightly convex, usually squarrose, orbicular-quadrate, .3-.45 mm long and wide, somewhat bilobed, usually with 4 or more blunt teeth or crenulations; vegetative reproduction by means of caducous leaves; dioicous; bracts of the female inflorescence suberect, broadly ovate, 1-1.3 mm long, .8-1.2 mm wide, usually crenate; perianth narrowly ovoid, 3 mm long, 1 mm in diameter, with 3 rounded keels; mouth contracted, minutely and irregularly spinulose-denticulate; male branches about .5 mm long and .4

mm wide; bracts mostly 4-6, strongly convex, apex minutely bidentate, antheridia solitary; bracteoles hardly .2 mm long, usually with 2 short blunt teeth; outer cells of capsule wall with thickenings, inner with semiannular thickenings; spores brownish green, 12-14 μ , minutely punctate; elaters bispiral, brownish, .2-.25 mm long, 8-10 μ thick. (Adapted from Evans).

Washington: Cascade Mountains, Montesano, upper valley of the Nisqually River, Pacific Beach, South Bend, Aberdeen, Hamilton, (22).

Oregon: Silverton (22).



Bazzania ambigua. 1. Part of plant, dorsal view, $\times 20$. 2. Part of plant, ventral view, $\times 23$. 3. Various forms of underleaves, $\times 27.5$. 4. Median leaf cells, $\times 178$. 5. Part of plant, ventral view; p, perianth, $\times 27.5$. 6. Leaf from short female branch, $\times 27.5$. 7. Three forms of bracts, $\times 27.5$.

2. *Bazzania tricrenata* (Wahlenberg) Pearson.

Plants green or yellowish brown, loosely to densely caespitose; stems 3-10 mm long, ascending, subpinnate to dichotomous, sometimes bearing flagella arising ventrally from axil of underleaves; rhizoids few on older part of stem, colorless; leaves imbricate, obliquely inserted, plane or convex, ovate-triangular, auriculate at base, .56-.8 mm long, .32-.4 mm wide, 1-3-toothed or -lobed; lobes unequal or subequal, short, acute or subobtuse; sinuses obtuse; margin entire; underleaves suborbicular, .21-.3 mm long, .28-.65 mm wide,

broadier than the stem, distant to imbricate; apex truncate, unequally 2-4-toothed; teeth short, ovate, obtuse; leaf cells nearly round, 15-36 μ ; walls thin; trigones large, triangular, distinct; cuticle finely granulate; dioicous; archegonial inflorescence terminal on short ovate branch; bracts larger than the leaves, irregularly divided; teeth obtuse; rhizoids at base of archegonial branch; perianth lanceolate-fusiform, 3-4 cells thick near the base, upper part contracted, plicate; mouth denticulate; antheridia terminal, more abundant than the archegonia, small, ovate, solitary; bracts 3-4 pairs; capsule ovate, of several layers of cells; spores brown, papillose.

Our specimens are almost all sterile. The species varies greatly in its leaves and underleaves. We believe with K. Mueller that it is not specifically distinct from *B. triangularis*. MacVicar is inclined to think the same altho he continues it as a species. *B. tricrenata* is the older name and is herein retained.

On wet rocks and trees in forests. Weston (Roell), 1888; Tacoma (Roell), 1888; Upper Skokomish River in Mason County (Piper), 1890; Seattle (Piper), 1891; Elwha River Valley (Frye), 1907; Yacolt (Frye), 1911; Chico (Frye), 1915; North Bend (Frye), 1926; Middle Fork of Snoqualmie River (Frye), 1926; Seattle (Bodenberg), 1928.

Idaho: Moscow Mountain (Clark), 1924.

LEPIDOZIA

Plants small to moderately large, yellowish green, often in dense mats with mosses; stems pinnately or subpinnately branched, often beautifully plumose; vegetative branches lateral, rarely ventral, often ending in flagella-like prolongations, from these often rhizoids springing; rhizoids few to many on the flagella; leaves incubous, small to large, convex dorsally, unsymmetric, incurved, usually as broad as long, 2-7-cleft, those subtending the branches when present 1-2-cleft; segments lanceolate; underleaves similar to the leaves but smaller and symmetric, segments with papillae at tip; first underleaf of a branch displaced to a position behind the branch; leaf cells medium sized or small; archegonia on short ventral branches; bracts delicate, 3-5 pairs, large-celled, translucent; apex denticulate; margin entire or denticulate or spinose; bracteoles similar; perianth free, fusiform or ovoid, in cross section triangular with the third angle ventral, contracted toward mouth; mouth denticulate to ciliate; androecium usually on short ventral branch, rarely on a lateral one; bracts suborbicular, bilobed,

sac-like; antheridia solitary; capsule cylindric, dehiscing to the base by 4 straight valves; walls 2-4-stratose; outer layer with nodular thickenings; inner cells with semiannular bands; seta moderately long; elaters with 2 spirals.

1. **Lepidozia reptans** (Linne) Dumortier.

Compared with *Bazzania* on page 124.

Plants pale or yellowish green, forming depressed mats or creeping among mosses; stems prostrate, 5-30 mm long, subpinnate to bipinnate, apices of branches obtuse or ending in flagella; leaves approximate or subimbricate or rarely distant, obliquely inserted, horizontal to erect-spreading, subquadrate, rarely ovate or obovate, .36-.45 mm long, .25-.54 mm wide, decurved, 3-4-cleft to $\frac{1}{3}$ - $\frac{1}{2}$ their length; lobes lanceolate or subulate, acute, unequal, incurved, 4-8 cells wide at base; underleaves present, distant or contiguous, subquadrate, broader than long, $\frac{1}{2}$ - $\frac{2}{3}$ the size of the stem-leaves, 4-lobed to the middle or below; lobes obtuse; leaf cells 24-48 μ ; walls firm; trigones obscure or distinct; cuticle smooth; autoicous; archegonial inflorescence terminal on short ventral branches; archegonia 2-6; bracts 2-3-lobed; margin entire or slightly denticulate; perianth subpyriform, narrowly obovoid-conic, 2-2.7 mm long, widest below the middle, more or less round to triangular in cross section, 2-3 layers thick at base, unistratose above, denticulate at mouth; androecia on short ventral branch; bracts 4-8 pairs, bilobed to $\frac{1}{3}$ their length; antheridia oblong, rarely on lateral branch; capsule ovate, 1-1.2 mm long, seta 1-2 cm long; spores 14-16 μ , distinctly granulate-papillate; elaters with 2 spirals, long.

On old logs, and in moist woods along banks of streams. Common in western Washington. Cascade Mountains (Allen), 1900; Ashford (Allen), 1900; Seattle (Frye), 1904; Olympic Mountains (Frye), 1907; Liberty Creek in Spokane County (Bonser), 1907; Westport (Foster), 1908; Coal Creek (Frye), 1909; Tacoma (Flett), year (?); Burlington (Clark), 1910, 1911; Olympic Mountains (Foster), 1911; Dungeness (Foster), 1913; Port Angeles (Foster), 1914; Chico (Frye), 1915; North Bend (Frye), 1921, 1927; Olga (Clark), 1925; north side of Orcas Island (Clark), 1925; Lakota (Clark), 1925; La Push (Frye), 1927.

Oregon: Powers Creek (Foster), 1910; Portland (44).

Idaho: Moscow Mountain (Clark), 1923.

Montana: Lake McDonald, Mt. Trilby, (40); Polson (Frye), 1928; Whitefish (Frye), 1928.

BLEPHAROSOTOMA

Plants small, slender and delicate; stems prostrate, entangled with mosses, branches usually lateral but sometimes subdichotomous; rhizoids few, colorless; leaves incubous, transversely inserted, distant or subimbricate, divided to base or nearly so into 2-5 rigid and setaceous or flaccid capillary segments; segments simple, rarely formed of a single row of cells thruout; underleaves present thruout, very similar to leaves; segments sometimes fewer by 1 and shorter; dioicous or paroicous; archegonial inflorescence terminal; bracts gradually larger than stem leaves, free from perianth, distinct or the inner slightly connate at the base; the often branched segments arising from a basal membrane several cells in height; bracteoles similar; archegonia few; perianth oblong to cylindrical, unistratose, ciliate at mouth; androecium terminal; bracts more crowded than the leaves; segments more numerous than on the stem leaves; antheridia ovoid, solitary; capsule dehiscing to base by 4 valves; elaters bispiral, obtuse.

Comparison of species of Anthelia, Blepharostoma and Ptilidium	Anthelia		Blepharostoma		Ptilidium	
	julacea p. 131	juratzkana p. 132	l. trichophyllum	s. arachnoidicum	californicum p. 133	pulcherrimum p. 135
Leaves cleft into 2 entire lobes.....	+	+	—	—	—	—
Leaves wholly split into cilia, or only partly so, or no cilia at all.....	n	n	w	w	p	p
Underleaves of 0, 2-5, or many cilia.....	0	0	2-5	2-5	m	m
Underleaves wholly split into cilia, or only partly so, or no cilia at all.....	n	n	w	w	p	p
Trigones bulging into the cells.....	—	—	—	—	+	+
Leaf how many ciliate, or many ciliate... Transverse walls of the cilia slightly projecting, slightly depressed.....	0	0	3-4 p	2-3 d	0-m	m
Length of plants in mm.....	5-15	1-4	4-20	5-10	10-50	5-20
Dioicous, paroicous.....	d	p	d		d	d
Number of spirals in elaters.....	2	3	2		2-3	2
Walls of leaf cells thick or thin.....	k	n	n	n	n	n
The 3-4 leaf lobes many ciliate or how many ciliate.....	×	×	1-2	1-2	1	m
Perianth ovate, oblong, obovate, pyriform, cylindric.....	1	v	c		1-b	p
Proportional depth to which leaf is notched.....	.4-.7	.4-.7	.9	.9	.6-.9	.5-.8

- A. Plants much branched; leaves divided into 3-4 capillary segments; leaf cells 40-70 μ long, 16-30 μ wide; transverse walls slightly protuberant. 1. *B. trichophyllum*
- AA. Plants little branched; leaves divided into 2-3 capillary segments; leaf cells 45-112 μ long, 25-51 μ wide; transverse walls slightly depressed. 2. *B. arachnoideum*

1. **Blepharostoma trichophyllum** (Linne) Dumortier.

Plants green or yellowish green, caespitose or among mosses; stems 4-20 mm long, abundantly branched; branches lateral; cortical stem-cells 28-96 μ long; rhizoids very rare; leaves approximate or distant, erect or spreading or suberect, divided nearly to base into 3-4 or rarely 2 to 5 capillary segments, .5-.96 mm long, .9 mm wide, connate to stem for $\frac{1}{2}$ - $\frac{3}{4}$ the length of the basal cells; leaf cells 40-70 μ long, 16-30 μ wide, 1.5-2.5 times as long as wide; transverse walls thickened outwardly so that the segments have protuberances thus giving them a nodose appearance; cuticle punctate or minutely striate; underleaves similar to the leaves, their segments 1-2 cells shorter; dioicous; female inflorescence on main stem or principal branch; bracts with 4-6 segments, basal membrane 2-6 cells high; segments antler-like; perianth, exserted, cylindric, 1.4-1.75 mm long, .4-.9 mm wide, with 1-2 furrows at apex; mouth wide, strongly contracted, connivent, ciliate; androecium terminal; bracts with narrow basal membrane; segments once forked; antheridia solitary, short stalked; calyptra thin, free, half as long as the perianth; capsule ellipsoid; valves bistratose; outer layer of cells with purplish brown columnar thickenings; inner layer with similar thickenings and semi-annular bands; seta 5-12 mm long; spores 14-18 μ , minutely papillate; elaters .13-.3 mm long.

On logs and moist soil. Roy (Allen), 1901; Paradise Valley on Mount Rainier (Frye), 1904; Hamilton (Foster), 1905; Queets and Elwha River Valleys (Frye), 1907; Wynooche (Foster), 1909; Burlington (Clark), 1912; Pacific Beach (Foster), 1911; Olympic Hot Springs (Foster), 1914.

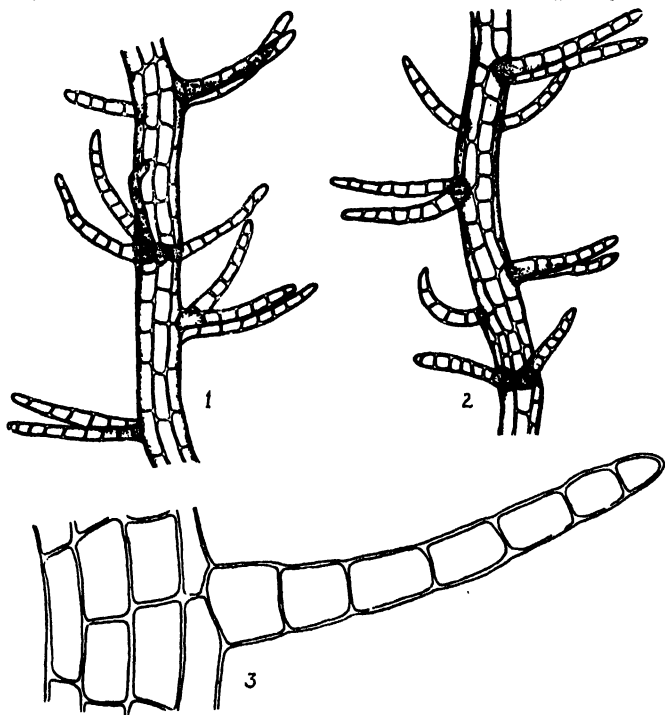
Idaho: Hope (35); Moscow Mountain (Clark), 1923.

Montana: Holzinger Basin, Mt. Trilby, (40); Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

Wyoming: Norris Geyser Basin, Craig's Pass, Mt. Washburn, all in Yellowstone National Park (Frye), 1925.

2. **Blepharostoma arachnoideum** Howe, Mem. Torrey Bot. Club 7:140. 1899.

Plants gray or yellowish green, densely depressed-caespitose; stems delicate, flaccid, ascending, 5-10 mm long, simple or sparingly branched; branches arising laterally or dichotomously, rarely ventrally; cortical stem-cells large, pellucid, inner cells smaller; rhizoids none or if present, long, colorless or yellow, arising singly or in groups from base of underleaves; leaves usually distant or subimbricate at apex, erect-spreading, .5-.96 mm long, divided to base or nearly so into 2-3 capillary segments, rarely on poorly developed stems with 1 segment; segments 1 cell wide, distant or sometimes connate with each other at base, usually forked about the middle; leaf cells elongated, about twice as long as broad, $45-112\ \mu$ long, $25-51\ \mu$ wide, hyaline thruout, slightly contracted at the transverse walls, rarely thickened, never protuberant at cross walls; trigones none; cuticle minutely striate; underleaves entirely similar to the leaves; gemmae often present at apex of stem giving it the appearance of being powdered, unicellular, about $25\ \mu$ in diameter, oblong-elliptic, formed



Blepharostoma arachnoideum. 1. Part of plant, dorsal view, $\times 82.5$. 2. Part of plant, ventral view, $\times 82.5$. 3. Part of stem and leaf, $\times 352$.

from the terminal cells of the segments, cells of the segments dividing into chains of 10-18 smaller cells; fructification unknown.

On old logs in moist woods. Hamilton (Foster), 1905; springs in mountains of Lewis County (Flett), 1905.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

ANTHELIA

Plants olivaceous or green or glaucescent (often thickly covered with a delicate white growth of fungal hyphae), slender, short, rigid or a long and flexible thread 1 μ in diameter; stems stout, opaque, irregularly pinnate; branches lateral thruout; cortical stem-cells many rows, small to large; rhizoids few or numerous; leaves incubous, transversely inserted, erect or erect-spreading, complicate-bilobed to middle or below; lobes subacuminate, several cells wide except at apex, margin entire or erose-denticulate; underleaves similar to lateral leaves, a little smaller, the stem appearing to have 3 rows of leaves; dioicous or paroicous; archegonia few, terminal on main stem or principal branch; bracts gradually becoming larger than leaves, densely imbricate, often denticulate, more or less fused at the base of the perianth; perianth ovoid to short-cylindric, deeply unisulcate dorsally, 2-3-carinate ventrally; mouth 8-10-plicate, slightly narrowed, lobate-dentate; wall 2-3 cells thick above, unistratose at base; androecium terminal; antheridia large, solitary in axil of bracts; calyptra 2-3 layers thick, carrying archegonia on surface, sometimes also with scale-like paraphyses; capsule subglobose, dehiscing to base by 4 valves; walls bistratose; outer wall with nodular and columnar thickenings; inner layer similar for lower half, apex with semiannular bands; seta short; elaters with 2-3 spirals.

- A. Plants 5-15 mm long; cell walls thick; dioicous; elaters with 2 spirals; perianth oblong. 1. *A. julacea*
 AA. Plants 1-4 mm long; cell walls thin; paroicous; elaters with 3 spirals; perianth ovate. 2. *A. juratzkana*

Species compared with Blepharostoma and Ptilidium on page 128.

1. *Anthelia julacea* (Linne) Dumortier.

Plants dark green or glaucescent or brownish, forming wide dense mats; stems prostrate, ascending or erect, 5-15 mm long, stout, julacent, irregularly pinnate, with subfloral innovations; rhizoids few, colorless, from base of stem; leaves imbricate, nearly transversely inserted, erect, incurved, ovate to oblong, .65-.7 mm long, bilobed to $\frac{1}{2}$ - $\frac{3}{4}$ their length; lobes lanceolate, subacute or acuminate or spiculate; sinus narrow; margin sinuate or subdenticulate; leaf cells rec-

tangular to quadrate, 24-51 μ long, 15-24 μ wide; walls thick; trigones none; cuticle smooth; underleaves similar to the leaves; dioicous; archegonial inflorescence terminal on main stem or branches; bracts larger than leaves, bilobed to $\frac{1}{3}$ - $\frac{1}{2}$ their length, plicate; lobes strongly toothed; perianth ovoid, about half exserted, 1-1.5 mm long, .6-.75 mm wide, deeply plicate from the middle up; mouth denticulate-lobed; androecium terminal; antheridia solitary, large, in axils of bracts; capsule subglobose, .49-.7 mm in diameter, brown; seta short; spores brown, 16-24 μ ; elaters with 2 spirals, brown, .12-.175 mm long, 11-14 μ wide.

On rocks in alpine regions. Mt. Rainier (Piper), 1895.

Oregon: Mt. Hood (45).

Montana: Sperry Glacier (40).

2. ***Anthelia juratzkana*** (Limpricht) Trevisan.

Plants green or glaucescent above, brown below, forming wide mats; stems prostrate, ascending or erect, 2-4 mm long, rather stout for the plant, irregularly pinnate; rhizoids few on the branches; leaves crowded, distant on sterile stems, ovate, .3-.35 mm long, bilobed to $\frac{1}{2}$ - $\frac{3}{4}$ their length; lobes lanceolate-ovate, acute or subacuminate; margin entire or slightly crose-denticulate; leaf cells rectangular, elongated-quadrate, 16-40 μ ; walls thin; trigones none; cuticle smooth; underleaves similar to the leaves; paroicous; archegonial inflorescence terminal; bracts several pairs, base saccate, apex denticulate; bracteoles present, similar to the bracts; perianth ovate, scarcely exserted, 1-1.6 mm long, .6-.7 mm wide; mouth somewhat constricted, lobate-denticulate; capsule .5-.7 mm in diameter; seta 1-3 mm long; spores 16-24 μ in greatest diameter, granulate-papillate; elaters .12-.175 mm long, 11-14 μ wide, with 3 spirals.

On rocks in alpine regions. Mount Rainier (Foster), 1905.

PTILIDIUM

Plants brownish green or dull green, forming dense mats; stems prostrate or ascending, 1-2-pinnate, irregularly and sparingly branched; the branches lateral; rhizoids few and short; leaves incubous, obliquely inserted, twice bifid to below middle or 3-5 times palmately cleft, dorsal segments larger; segments long, slender, acuminate, rarely entire, usually fringed with long simple or branched cilia; underleaves smaller but similar to leaves, 2-3-parted; archegonia terminal on main stem or principal branch; perianth because of subfloral innovations appearing apical on short lateral or dichotomous divergent branch; bracts 1-2 pairs, similar to leaves, more ciliate-lacinate; per-

ianth free, several times larger than bracts, cylindric-obovate; mouth contracted, ciliate-plicate; androecium terminal on main stem or principal branch; bracts more concave, more closely imbricate than leaves; antheridia short stalked; capsule ovoid, on a long stalk, dehiscing to base by 4 rigid valves; cells with semiannular rings and nodular thickenings; spores punctate, several times broader than elaters; elaters with 2 or rarely 3 spirals.

A. Leaf lobes commonly 1-2-ciliate.

1. *P. californicum*

AA. Leaf lobes commonly many ciliate.

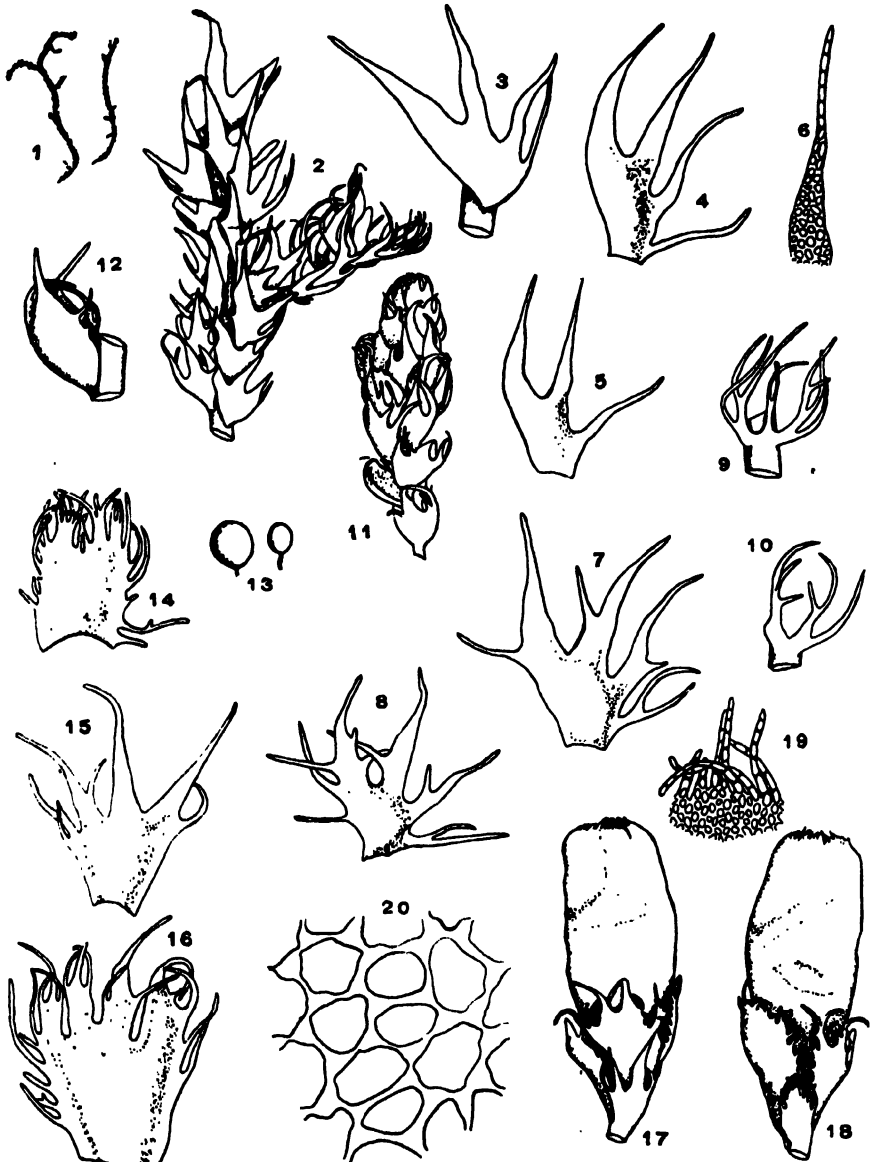
2. *P. pulcherrimum*

Species compared with *Blepharostoma* and *Anthelia* on page 96.

1. ***Ptilidium californicum*** (Austin) Underwood and Cook.

Plants bright green or reddish brown, densely depressed-caespitose; stems creeping and ascending at apex, 1-5 cm long, irregularly subpinnate; rhizoids wanting or very few; leaves imbricate, transversely inserted, complicate-bilobed, palmately divided into 3-4 segments for 2/3-5/6 their length; segments linear-lanceolate or lanceolate, long, slender, unequal, 2 dorsal ones larger, 1-2 ventral ones smaller and subinflexed; margin ciliate, repand or entire; sinuses obtuse; leaf cells 30-60 μ ; walls thin; trigones very large; cuticle smooth; underleaves wider than the stem, 2-3-cleft, their segments incised-ciliate; dioicous; archegonial inflorescence on a short lateral branch; bracts 1-2 pairs, larger than the leaves, less deeply lobed, more densely incised-ciliate; bracteoles similar to underleaves, rarely united with the bracts; perianth cylindric-obovate to subfusiform-oblong, base obconic, upper part slightly contracted; mouth ciliate, plicate; androecia on more slender plants, terminal on main stem or principal branch; antheridia ovoid or elliptic, single or in pairs, final stalks shorter than their own diameter; spores light brown, densely punctate, 21-30 μ ; elaters .120-.225 mm long, 7-10 μ thick, with 2 or rarely 3 spirals.

On trees in dry places. Seattle (Piper), 1890; Spokane (Piper), 1901, (Bonser), 1907; Paradise Valley on Mount Rainier (Flett), 1904, (Foster), 1909; Hamilton (Foster), 1905; Mount Constitution (Frye), 1905; Mount Carlton trail in Spokane County (Bonser), 1907; Cathlamet (Foster), 1907; Elwha River valley in Olympic Mountains (Frye), 1907; Halls Lake near Edmonds (Frye), 1909; Ashford (Allen), year (?); Pacific Beach (Foster), 1911; Dosewallups River (Foster), 1911; Port Angeles (Foster), 1911; Mt. Ellinor (Foster), 1912; Gate (Foster), 1912; Lake Cushman (Foster), 1912; Chico (Frye), 1915; Lake Kechelus (Frye), 1921; Friday Harbor



Ptilidium californicum. 1. Plants, natural size. 2. Part of plant, $\times 12$. 3. Stem leaf, dorsal view, $\times 23$. 4. Stem leaf, ventral view, $\times 23$. 5. 3-cleft stem leaf, ventral view, $\times 23$. 6. Typical apex of leaf-segment, $\times 41$. 7. Stem leaf, ventral view, $\times 23$. 8. Branch leaf, ventral view, $\times 23$. 9-10. Underleaves, $\times 23$. 11. Androecium, $\times 12$. 12. Male bract, $\times 23$. 13. Antheridia, $\times 23$. 14. Bracteole, $\times 23$. 15. Next to inmost bracteole, $\times 23$. 16. Inmost bracteole, $\times 23$. 17. Ventral view of perianth and bracts, $\times 12$. 18. Dorsal view of perianth and bracts, $\times 12$. 19. Portion of perianth mouth, $\times 41$. 20. Leaf cells, $\times 225$. (Figs. 1-6, 9, 10 after Howe; remaining figures after Leiberg).

(Clark), 1923; north side of Orcas Island (Mullen), 1925; Darrington (Frye), 1928. Here probably belong the collections by Roell in 1888 which Stephani referred to *Ptilidium ciliare*, from Enumclaw, Weston, Cascade Mountains, Lake Kechelus, Easton; also his from Montana.

Oregon: Mt. Hood (29); Powers Creek (Foster), 1910; Albany (Van Wert), about 1923.

Idaho: Hope (35); Moscow Mountain (Clark), 1923.

Montana: Mt. Trilby (40); Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928; Wolf Creek (Frye), 1928; Polson (Frye), 1928; Whitefish (Frye), 1928; Belton (Frye), 1928; Libby (Frye), 1928.

2. *Ptilidium pulcherrimum* (Weber) Hampe.

Plants small, in very dense patches, yellowish brown or rarely reddish brown; stems prostrate with ascending apices, irregularly and abundantly branched; branches short; leaves closely imbricate, transversely inserted, concave, roundish-quadrangle, divided into 4 lobes for $2/3$ - $5/6$ the leaf-length; lobes narrowly lanceolate, margin densely ciliate, incurved; leaf cells $28-36 \mu$; trigones large; cuticle smooth; underleaves about half as large as the leaves, deeply divided into 2 segments; segments lanceolate, ciliate; cilia long, incurved; dioicous; female inflorescence terminal on main stem or branch, later appearing lateral thru innovations; bracts embracing the perianth, concave, divided for $1/3$ - $1/2$ their length into 2-4 lobes; margins densely ciliate; perianth large, long exserted, swollen, pyriform, plicate above, obtuse; mouth contracted, 4-5-lobed, ciliate; male inflorescence terminal on main stem, bracts in several pairs, smaller than the leaves, ventricose, unequally 3-4-lobed, with incurved cilia; antheridia 1-2, large, without paraphyses; capsule subglobose, dark brown, inner wall with semiannular thickenings; spores brown, finely papillose; elaters bispiral, reddish brown.

On stems of trees or on ground among trees, rarely on rocks, Republic (Foster), 1912.

Idaho: Genesee Ridge near Moscow (Clark), 1923.

Montana (9).

DIPLOPHYLLUM

Plants yellow or brown or green, depressed-caespitose or creeping among mosses; secondary stem leafy, robust or delicate, simple

Comparison of species of <i>Diplophyllum</i>	1. albicans	2. taxi- folium	3. obtusifolium	4. ovatum
Ventral leaf lobe with median elongated cells simulating a vein.....	+	—	—	—
Tip of leaf lobe obtuse, acuminate, acute, apiculate; the dorsal..... The ventral.....	o-t o-t	o-t-p o	o-t o-p	m m
Isodiametric leaf cells of ventral lobes in μ	12-15	10-18	16-20	20-25
Trigones small, none.....	n	n	n	s
Length of marginal teeth of ventral lobes as measured in cells.....	.5-1.5	1-2	0.8	×
Dioicous, paroicous.....	d	d	p	d
Cuticle smooth, striate, verruculose.....	m-t	v	v	m-v
Ventral lobes how many times as long as the dorsal.....	1.5-2	2-2.5	2-3	1.5-2
Rhizoids fairly numerous, scarce.....	s	s-n	n	n
Margin of leaf lobe denticulate, entire, crenulate; the dorsal..... The ventral.....	d-e d	d d	d-e d-e	c-e c-e

- A. Ventral lobe of leaf with elongated cells along its middle and resembling a vein; cuticle nearly smooth. 1. *D. albicans*
- AA. Ventral lobe of leaf without the vein-like appearance; cuticle usually rough.
- B. Ventral lobes of leaf rounded or obtuse; dorsal leaf lobe rounded to acute.
- C. Leaf cells 10-16 μ ; plant dioicous. 2. *D. taxifolium*
- CC. Leaf cells 16-20 μ ; plant paroicous. 3. *D. obtusifolium*
- BB. Ventral and dorsal leaf lobes both acuminate. 4. *D. ovatum*

1. **Diplophyllum albicans** (Linne) Dumortier.

Secondary stems brown or green, caespitose or loosely creeping in mats; stems 1-4 cm long, erect or prostrate with ascending apex, 3-4-pinnate or simple; rhizoids few, long, colorless; leaves subimbricate to imbricate, transversely inserted, alternate, complicate-bilobed to or beyond the middle; lobes unequal; dorsal lobe 1/2-2/3 as large as ventral, appressed, ascending, nearly parallel to the stem, obtuse or seldom acute at apex; ventral lobe .56-.98 mm long, .168-.37 mm wide, oblong-ovate, spreading at nearly right angles to the stem, obtuse or rarely acute at apex, margin denticulate; cells of median part of ventral lobe in 4-6 or rarely more rows of elongated rectangular cells forming a false vein, their longitudinal walls thick, their cross walls thin; remainder of cells rotund-quadrangle, 12-15 μ ; walls uniformly thickened; trigones none; cuticle more or less striate; gemmae occurring at apex of antheridial plants, golden brown, star-shaped; dioicous; archegonial inflorescence terminal on main stem; bracts 1-2 pairs, similar to leaves, larger; ventral lobe orbicular, strongly toothed; lobule near base of each lobe; perianth oblong, inflated, exerted for most of its length, plicate in upper part; mouth ciliate-dentate; androeia on short innovations; bracts concave, inflated; antheridia borne in inflated base of ventral lobe; capsule brown, oblong, on a long delicate seta, of 2 layers of cells; spores light brown, round, 10-12 μ , finely papillose; elaters bispiral, brown.

On wet rocks. Mt. Rainier (Piper), 1895; Queets River valley (Frye), 1907; Westport (Foster), 1908; Aberdeen (Foster), 1909; North Bend (Frye), 1921.

Oregon: Powers Creek (Foster), 1910; Cape Arago (Frye), 1922.

2. *Diplophyllum taxifolium* (Wahlenberg) Dumortier.

Plants green or yellowish brown, forming depressed caespitose mats; stems prostrate or ascending, simple or sparingly branched; branches arising from base of leaves; rhizoids wanting or few; leaves subtransversely inserted, distant or approximate or imbricate, appressed at base, spreading above, complicate-bilobed to $2/3$ their length; keel slightly arched; dorsal lobe erect-spreading, or subacute or apiculate at apex, sharply and irregularly dentate at margin, .4-.72 mm long, .25-.28 mm wide; ventral lobe widely spreading, oblong or obovate, obtuse or rounded, .91-1.1 mm long, .27-1.42 mm wide, twice as large as dorsal, its margin irregularly dentate, teeth of margin 1 or rarely 2 cells long; leaf-cells small, rotund-quadrate, 10-18 μ , basal cells elongated but not forming a vein; walls uniformly thickened; trigones none; cuticle verruculose; gemmae on sterile plant broadly fusiform, of 1-3 cells; dioicous; archegonial inflorescence terminal on main stem; bracts 1 pair, similar to leaves but more erect; margin more entire; perianth ovate-cylindric, 3-3.5 mm long, .9-1 mm wide, narrowed abruptly toward mouth with 15-16 subacute or subobtuse folds, otherwise terete thruout; mouth deeply plicate, irregularly lacerate, the divisions subentire or crenulate-denticulate; androecium median on stem or branch; bracts imbricate, many pairs, similar to leaves but saccate at base, dorsal lobes more erect; antheridia 2 to a bract; capsule brown and oval; spores light brown, densely minutely papillate, 21-30 μ .

On wet soil. Easton (Roell), 1888. Lake Kechelus (Roell), 1888; Snoqualmie Pass (Piper), 1891; Stevens Pass (Sandberg and Leiberg), 1893; Paradise Valley on Mount Rainier (Frye), 1904; Elwha River Valley in Olympic Mountains (Frye), 1907; Quinault Indian Reservation (Foster), 1908; Mount Rainier (Foster), 1909; Montesano (Foster), 1910; Pacific Beach, (Foster), 1910, 1911; North Bend (Frye), 1926; Darrington (Frye), 1928.

Idaho (11).

3. *Diplophyllum obtusifolium* (Hooker) Dumortier.

Plants reddish green or green, densely caespitose; stems erect or ascending, small, 3-6 mm long, simple or rarely laterally branched; rhizoids fairly numerous, long, colorless, numerous at apex; leaves subimbricate to imbricate, complicate-bilobed to below middle; dorsal lobe horizontal, making an angle of about 10 degrees with the stem, ovate or oblong, obtuse or acute, erect, margin denticulate or entire; ventral lobe 2-3 times larger than dorsal; oblong-obovate and arcuate.

slightly concave, obtuse or rarely apiculate, minutely toothed or entire at margin, teeth $\frac{1}{2}$ - $\frac{3}{4}$ of a cell long; leaf cells quadrate, 16-20 μ , elongated at base of ventral lobe but not forming a vein; walls equally thickened; trigones distinct; cuticle verruculose; paroicous; archegonial inflorescence terminal on main stem; bracts similar to leaves but larger; perianth exserted $\frac{1}{3}$ - $\frac{1}{2}$ beyond bracts, obovate or ovate, upper part plicate with 5 folds; mouth contracted, denticulate; androecia median on main stem or subfloral innovations; antheridia at base of archegonial bracts; antheridial leaves saccate containing 1-2 small antheridia.

On wet rocks. Seattle (Piper), 1891; Pacific Beach (Foster), 1911; Snoqualmie Pass (Frye), 1921; Mt. Constitution (Peterson), 1925.

Oregon: Newport (Daugherty), 1921.

4. **Diplophyllum ovatum** (Dickson) Stephani, Spec. Hep. 4:110. 1910.

Jungermannia ovata Dickson, Pl. Crypt. Brit. Fasc. 3:11. 1793.

Jungermannia dicksoni Hooker, Brit. Jungerm., pl. 48. 1813.

Diplophyllum dicksoni Dumortier, Rec. d'Observ., p. 16. 1835.

Lophozia ovata Howe, Mem. Torrey Bot. Club 7:111. 1899.

Sphenobolus ovatus Schiffner, Krit. Bemerkungen zu Ser. 4 der Hep. Europ. Exsic. "Lotos" No. 3:60. 1905.

Plants in thick brownish green to yellowish green mats; stems prostrate or ascending, 8-20 mm long, simple or dichotomous; rhizoids long, present to stem apex; leaves imbricate, transversely inserted, bilobed to below middle; lobes unequal, lanceolate, acuminate, entire or crenulate toward apex; dorsal lobe suberect, somewhat parallel to stem; ventral lobe ovate to oblong-ovate, spreading-horizontal, twice as large as dorsal lobe; leaf cells roundish in middle, 20-25 μ , elongated at base but not forming a vein; walls firm; trigones present; cuticle minutely roughened or smooth; dioicous; bracts somewhat larger than the leaves, long acuminate, sparingly dentate; bracteole small, lanceolate; perianth oval to oblong, 2-3 times as long as bracts, deeply plicate, mouth ciliate-lacinulate; capsule reddish brown, oval; spores yellowish brown, 15 μ wide, with short spines; elaters 8-12 μ broad, unispiral or with ring-like thickenings.

On shaded rocks. Darrington (Frye), 1928.

Oregon: Seaside (23).

SCAPANIA

Plants large, green or brown or rose-red or purple, primary stem without leaves, creeping; secondary stem ascending, erect, rarely prostrate, simple or dichotomous, apex often decurved; leaves alternate, in

2 or rarely 3 rows, complicate-bilobed; keel more or less winged, acute; fold archings outward; margin of lobes entire or dentate or ciliate; dorsal lobe incumbent; ventral lobes larger than dorsal, convex dorsally, succubous; underleaves none; gemmae often present on stem apex and upper stem leaves; dioicous or rarely monoicous; archegonial inflorescences terminal on main stem, few; bracts scarcely differing from leaves, a little larger, subequally lobed; perianth oblong or obovate, strongly compressed dorsi-ventrally, smooth or rarely sub-plicate; mouth broad, truncate, entire or ciliate or dentate, commonly decurved when young; androecium terminal or median; bracts hardly differing from leaves, ventricose, a little smaller, lobes subequal; antheridia 1-6, ovoid or elliptic, stalked, often with hair-like or leaf-like paraphyses; capsule oblong-ovoid, long-exserted.

A. Basal margin of dorsal leaf lobe with long compound cilia.

2. *S. bolanderi*

AA. Basal margin of dorsal leaf lobe entire or with small teeth.

B. Lobes of the leaves equal or nearly so, their margins entire to denticulate; dorsal lobe arching beyond the stem.

11. *S. uliginosa*

Comparison of species of Scapania	1. subal- pina	2. bolan- leri	3. undu- lata
Dorsal leaf lobes equal to ventral or nearly so.....	+	—	—
Dorsal lobes long decurrent.....	—	—	—
Basal margin of dorsal lobe with compound cilia . . .	—	+	—
Ventral lobes long decurrent.....	+	±	+
Ventral lobes entire, undulate only, with only a few teeth at tip, much toothed.....	e-m	m	u
Dorsal lobes distinctly arching beyond the stem	+	+	+
Tips of ventral lobes acute, obtuse, rounded	r	o	o-r
Dorsal lobes longer than wide, as long as wide, wider than long.....	w	a-w	l
Keel winged.....	—	+	±
Keel entire or toothed.....	e	e-t	e
Cuticle papillose, verruculose, minutely roughened, smooth.....	p	m	m
Trigones large, small, none.....	s-l	l	n
Tip of dorsal lobe acute, obtuse, rounded.....	o	a-r	o
Dorsal lobe entire.....	±	—	—
Length of median leaf cells in mu.....	18-30	15-30	36-60
Proportional depth to which leaves are cleft.....	.5	.5-.7	.5-.7

BB. Lobes of the leaves unequal.

C. Ventral lobes of the leaves entire or undulate, or very sparingly dentate toward the apex.

D. Dorsal lobe reniform, convex, long decurrent, $\frac{1}{3}$ - $\frac{1}{2}$ the size of the ventral lobe, rounded at apex.

11. *S. uliginosa*

DD. Dorsal lobe not reniform, not long decurrent, about $\frac{1}{2}$ the size of the ventral lobe, acute to obtuse.

E. Ventral lobes entire or with a few teeth at tip, not or little decurrent; dorsal lobes not distinctly arching beyond the stem, acute; trigones small; median leaf cells 12-36 μ long.

F. Stems 2-5 cm long; rhizoids rather scarce; dorsal leaf lobes wider than long; mouth of perianth not ciliate.

9. *S. irrigua*

FF. Stems 1-2 cm long; rhizoids numerous; dorsal leaf lobes longer than wide; mouth of perianth somewhat ciliate.

10. *S. curta*

4. nemo- rosa	5. dentata	6. oakesii	7. umbrosa	8. evansii	9. irrigua	10. curta	11. uligi- nosa	12. cordi- folia
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	+	+
—	—	—	—	—	—	—	—	—
+	+	—	—	—	—	—	+	—
m	m	m	m	m	e f	e-f	e	m
+	—	+	—	—	—	—	—	+
o	o-r	a-o	a-o	r	a-o	a-o	r	o-r
w	a	w	a-l	w	w	a-l	w	w
\pm c	+	\pm t	— c	+	\pm c	— c	— e	— e
m n	m s	m s	m s	p l	m s	m s	s-m s-n	v s
r — 12-30 .7-.8	a \pm 15-24 .5-.7	a-r — 15-24 .5	a — 12-30 .7	a-o — 24-32 .5	a \pm 19-24 .4-.5	a \pm 12-36 .4-.5	r + 20-30 .5-.7	a-o — 20-45 .5

- EE. Ventral lobes undulate, strongly decurrent; dorsal lobes distinctly arching beyond the stem, obtuse or rounded; trigones none; median leaf cells 36-50 μ long. 3. *S. undulata*
- CC. Ventral lobes of the leaves much toothed.
- G. Ventral lobes long decurrent.
- H. Ventral lobes ciliate; trigones none. 4. *S. nemorosa*
- HH. Ventral lobes dentate; trigones small. 5. *S. dentata*
- GG. Ventral lobes not long decurrent.
- I. Dorsal lobes not arching beyond the stem.
- J. Ventral lobes acute to obtuse; trigones small; keel about .7 the length of the leaf. 7. *S. umbrosa*
- JJ. Ventral lobes rounded at tip; trigones large; keel about .5 the length of the leaf. 8. *S. cavausii*
- II. Dorsal lobes distinctly arching beyond the stem.
- K. Dorsal lobes not long decurrent; median leaf cells 15-24 μ long; ventral acute to obtuse. 6. *S. oakesii*
- KK. Dorsal lobes long decurrent; median leaf cells 20-45 μ long; ventral lobes obtuse to rounded. 12. *S. cordifolia*

1. **Scapania subalpina** (Nees) Dumortier.

Plants dark green or brown, in loose mats or creeping among mosses; stems erect or ascending, .5-5 cm long, apex decurved, lower part nearly devoid of leaves, simple or sparingly branched; rhizoids few, long, colorless; leaves distant to imbricate, increasing in size toward apex, complicate-bilobed for $\frac{1}{4}$ - $\frac{1}{3}$ their length; keel very slightly winged, entire; dorsal lobe oval-orbicular or triangular, .5-.7 mm long, .065-.5 mm broad, arching over stem, ascending or appressed, obtuse or broadly narrowed, margin undulate or entire or denticulate; ventral lobe oval-suborbicular, .9-1.4 mm long, .9-1.1 mm broad, 1-1.3 times as large as the dorsal lobe, spreading, decurrent, rounded, margin subentire or undulate-denticulate; leaf cells quadrate to subrotund, 18-30 μ , basal cells elongated so as to form a very indistinct vein; walls thin; trigones small, or large and confluent; cuticle with hyaline papillae 3-12 μ long, 2-6 μ wide, number varying with size of cell, in large ones 11-20; gemmae yellowish green or sometimes violet, oval, 2-celled; dioicous; archegonial inflorescence terminal; androecium terminal on main stem; bracts similar to leaves, saccate; antheridia 1-3; perianth oblong; mouth truncate, sinuate and

denticulate; teeth somewhat distant; capsule oval; inner wall with numerous nodular and incomplete or rarely complete semiannular thickenings; spores $20\ \mu$, reddish brown, finely punctate; elaters bispiral, $6\ \mu$ thick. The perianth, capsule, spores and gemmae are lacking in our material, and their description is adapted from MacVicar.

On wet rocks, Elwha River valley in Olympic Mountains (Frye), 1907.

This also occurs in Colorado (31) and is likely to be found on high mountains rather generally in our area.

2. **Scapania bolanderi** Austin, Proc. Acad. Nat. Sci. Philadelphia 1869:218. 1869.

Scapania californica Gottsche, Calif. Med. Gaz. 1870:184. 1870.

Scapania albescens Stephani, Bot. Jahrb. 8:96. 1886.

Plants dark olive-green or yellowish brown, densely caespitose; stems rigid, erect or ascending or prostrate or subpendulose, 1-8 cm long, simple or dichotomous, sometimes with subfloral innovations; leaves imbricate to distant, stiff, hardly changing shape on drying, complicate-bilobed; keel acute, entire or rarely with a single tooth; dorsal lobe more or less imbricate, appressed or erect, broadly ovate, .6-1 mm long, .7-.78 mm broad, convex subacute, irregularly dentate, teeth larger than those of ventral lobe, at base with several curved single or compound cilia; ventral lobe erect, obliquely oblong-ovate, strongly convex, obtuse, slightly decurrent, coarsely dentate, $2\frac{1}{2}$ times as large as dorsal, 1.1-1.7 mm long, .75-.8 mm broad; apex and ventral margin deflexed; leaf-cells subquadrate-oval, median 15-30 μ ; basal



Scapania bolanderi. 1. Portion of sterile plant, dorsal view, $\times 6$. 2. Leaf, ventral view, $\times 11.5$. 3. Leaf, dorsal view, $\times 11.5$. 4. Ciliate margin of base of dorsal lobe, $\times 53$. 5. Apex of ventral lobe, $\times 53$. 6. Leaf cells near tip of ventral lobe, $\times 152$. (After Howe).

cells elongated; trigones very conspicuous in basal cells; cuticle minutely roughened; dioicous, both plants occurring in same mat; archegonial inflorescence terminal on main stem; bracts 1-2 pairs of slightly modified leaves, saccate; antheridia 2-6, elliptic-ovoid, stalked; stalks equal to or longer than antheridia; paraphyses numerous, branching; capsule brown, oblong-ovoid; seta 3-10 mm long, spores 10-12 μ ; elaters contorted, .1-.175 mm long, 8-10 μ thick.

On logs and stumps of conifers; very common in western Washington. Easton (Roell), 1888; Cle Elum Lake (Roell), 1888; Enumclaw (Roell), 1888; Weston (Roell), 1888; Seattle (Piper), 1890, also 1891; Cascade Mountains (Allen), 1900; Seattle (Frye), 1904; Hamilton (Foster), 1905; Snoqualmie Falls (Frye), 1906; Bellingham (Romine), 1907; Elwha River Valley (Frye), 1907; Westport (Foster), 1908; Ilwaco (Frye), 1908; South Bend (Frye), 1908; Nahcotta (Frye), 1908; Halls Lake near Edmonds (Frye), 1909; Exposition Gulch in Tacoma (Flett), year (?); Lacenter (Davis), year (?); Burlington (Clark), 1910, 1922; Kalama (Frye), 1911; Copalis Rocks (Foster), 1911; Yacolt (Frye), 1911; Port Angeles (Foster), 1914; Granite Falls (Frye), 1921; Friday Harbor (Smith), 1923; Olga (Clark), 1925; North side of Orcas Island (Peterson), 1925; Fairfax (Frye), 1925; junction of White and Greenwater Rivers (Frye), 1926; North Bend (Frye), 1926; La Push (Frye), 1927.

Oregon: Astoria (45); Rainier (31); Portland (44); Powers Creek (Foster), 1910; Cape Arago (Frye), 1922; Santiam National Forest (Van Wert), about 1923.

3. *Scapania undulata* (Linne) Dumortier.

Plants olive-green or brown or reddish purple, in loose mats; stems 1-10 cm long, rigid and erect or sometimes floating, lower portion leafless and brittle; rhizoids long, colorless, few; leaves distant, approximate to closely imbricate, larger above, sometimes soft and flaccid, on drying becoming crumpled or undulate, ciliate-dentate or entire or denticulate; keel more or less winged, entire; dorsal lobe obliquely and broadly ovate, sometimes slightly bent toward or away from stem, arching beyond stem, slightly or not at all decurrent, .7-1.4 mm long, .56-1.2 mm broad, apex subobtuse; margin entire; ventral lobe nearly twice the size of the dorsal, round-trapezoidal, 1.1-1.9 mm long, .84-2.1 mm broad, flat or convex, decurrent, apex obtuse or rounded or rarely broadly pointed, margin undulate; median leaf cells polygonal, 36-60 μ long, 15-30 μ wide; marginal cells quadrate, 12-30 μ ; walls thin, colorless or pigmented; trigones none; cuticle

more or less roughened with minute hyaline papillae; gemmae in clusters at apex of stem, 1-2-celled; dioicous; archegonial inflorescence terminal; bracts similar to leaves; perianth oblong; mouth slightly narrowed, entire repand or subdentate; androecium terminal; bracts smaller than leaves, saccate, 4-5 pairs; antheridia elliptic to suborbicular, 3-5 in axil of leaf; paraphyses present, numerous, multicellular, simple; capsule elliptic, dark-brown, exserted; spores brown.

On stones, in streams and in very moist places especially in mountains. Mt. Rainier (Piper), 1895; Stevens Pass (Sandberg and Leiberg), 1895; Paradise Valley on Mt. Rainier (Frye), 1904; Ashford (Allen), 1904; Queets River valley in Olympic Mountains (Frye), 1907; Suiattle Trail in Glacier Peak region (Winona Bailey), 1910; Buck Creek in Glacier Peak region (Winona Bailey), 1910; Mt. Angeles (Frye), 1927.

Oregon: Snow Mountain in Santiam National Forest (Van Wert), about 1923.

Idaho: Bonners Ferry (Frye), 1928.

Montana: Holzinger Basin, Lake McDonald, (40); Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

Wyoming: Near Giant Paint Pot in Yellowstone National Park (Frye), 1925.

4. *Scapania nemorosa* (Linne) Dumortier.

Plants brown or olive green, sometimes tinged with red, usually caespitose or in loose mats with mosses; stems 1-6 cm long, rigid, ascending, apex commonly decurved, sparingly branched; rhizoids colorless, very few; leaves approximate or slightly imbricate, bilobed for $\frac{3}{4}$ their length, both lobes ciliate-dentate; keel more or less winged; dorsal lobe reniform or obliquely ovate, 1.16-1.68 mm long, .9-1.1 mm broad; apex rounded or apiculate, usually a little arched; margin appressed; ventral lobe obovate, 2-2.5 times as large as dorsal lobe, 1.33- 2.1 mm long, .84-1.12 mm broad; apex obtuse, a little deflexed, convex; margin slightly reflexed, decurrent; leaf cells rotund-quadrangle, 12-30 μ ; walls thick; trigones none; cuticle roughened with small warts; gemmae borne at stem apex or at margins of leaves, yellowish brown, oval, of 1-2 cells; dioicous; archegonial inflorescence terminal; bracts similar to leaves; perianth long-obovate; 2.5-3.6 mm long, 1.1-2 mm broad; mouth subpiculate, truncate, ciliate-dentate; androecium terminal; bracts similar to leaves, saccate; antheridia 3-6, with numerous paraphyses which occur also on other parts of the stem; paraphyses long, multicellular, simple or branched, hair-like; capsule brown, ovoid-

oblong; stalk 3-10 mm long; spores 12-16 μ , brown-punctate; elaters contorted, brown, .1-.18 mm long, 7-10 μ thick.

On rocks and soil. Easton (Roell), 1888; Renton (Frye), 1904; Hamilton (Foster), 1905; Summit (Foster), 1907; Westport (Foster), 1908; Lacenter (Davis), year (?); Pacific Beach (Foster), 1911; north side Orcas Island (Clark), 1923; Mt. Angeles (Frye), 1927; Darrington (Frye), 1928.

Oregon: Hult (Foster), 1910; Portland (Flinn), 1912.

Idaho: Moscow Mountain (Clark), 1923.

Montana: Lake McDonald, Sperry Glacier region, (40).

Wyoming: Craig's Pass in Yellowstone National Park (Frye), 1925.

5. *Scapania dentata* Dumortier.

Plants more or less tinged with red or purple, densely caespitose, sometimes bright-green or brownish; stems rigid, erect, 1-3.5 cm long, simple or sparingly branched; rhizoids none or very few; leaves distant, approximate to closely imbricate on female stems where they are larger, transversely inserted, bilobed for 2/3 their length; keel winged; wing with or without curved teeth especially on archegonial stems; dorsal lobe rarely imbricate except at apex, rarely crossing the stem, not decurrent, rotund-ovate, convex, rounded to subacute; margin of upper ones dentate, lower ones entire or sparingly dentate; teeth smaller than those of ventral lobe; ventral lobe obliquely obovate or rhombic, 2-3 times larger than the dorsal, convex, obtuse or rounded or rarely pointed, serrate-dentate or nearly entire; teeth 1-2 celled; margin decurrent; leaf cells median 15-24 μ long, elongated ones 30-54 μ long and 15-18 μ broad; trigones indistinct; walls uniformly thickened or thin; cuticle distinctly or obscurely roughened; dioicous; archegonial inflorescence terminal; bracts similar to leaves, a little larger; perianth oblong to obovate, truncate; mouth denticulate to sinuate or subentire; androecium terminal or appearing median by innovations; bracts distinct, approximate to subimbricate, smaller than leaves, ventricose; lobes somewhat equal; keel entire, rarely toothed; antheridia 2-6; paraphyses usually present, short, capillary; capsule oval, brown; seta long; spores reddish-brown, 15-18 μ , papillate; elaters brown or reddish, contorted, .12-.18 mm long.

On wet logs and rocks. Paradise Valley on Mt. Rainier (Flett), 1904; Hamilton (Foster), 1905; Granite Falls (Frye), 1921.

Oregon: Cape Arago (Frye), 1922.

Idaho: Moscow Mountain (Clark), 1924.

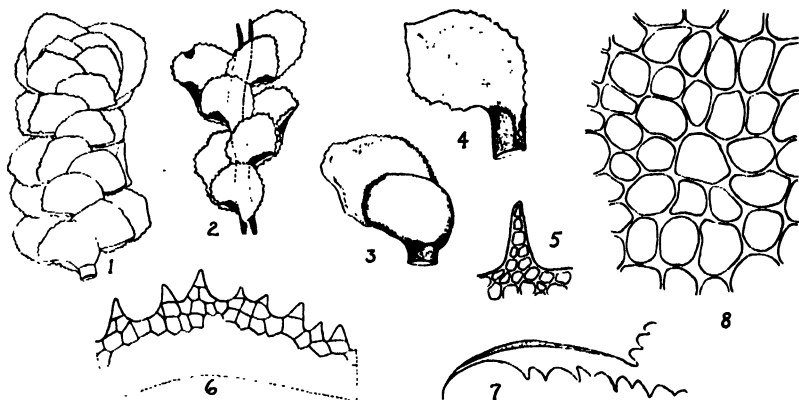
Montana (9).

Wyoming: Near Roaring Mountain in Yellowstone National Park (Frye), 1925.

6. *Scapania oakesii* Austin, Bull. Torrey Bot. Club 1872:10. 1872.

Scapania dentata oakesii K. Mueller, Scapania-Monographic, p. 102. 1905.

Plants in green brownish or purple caespitose mats; stems rigid, brown, simple or sparingly branched, ascending or erect, 1-2.5 cm long; rhizoids few; leaves approximate to close crowded and larger at apex of female plants, more or less flaccid or rigid, keeled; keel in upper leaves and archegonial bracts broad, with 1-2 series of long curved teeth, wanting or few on male plants, ventral margin decurrent; ventral lobe obovate, 2-2.5 times as large as dorsal one, obtuse or



Scapania oakesii. 1. Portion of female plant, dorsal view, X6. 2. Portion of plant, dorsal view, X6. 3. Leaf from lower part of stem, dorsal view, keel entire, X11.5. 4. Leaf, ventral view, X11.5. 5. Marginal tooth of leaf, X120. 6. Margin at apex of ventral lobe, X106. 7. Keel of leaf, with toothed wing, X60. 8. Leaf cells from near apex of ventral lobe, X305. (1, 3, 4, 6, 8, after Howe; 2, 5, 7, after K. Mueller),

sometimes acute, serrate-dentate; dorsal lobe round ovate, imbricate at apex, convex, obtuse or subacute, upper ones often with a tooth at basal margin, other teeth smaller and less numerous than on ventral lobe; cells oblong-hexagonal at base, marginal and median cells quadrate-ovate 15-24 μ ; walls thickened; trigones indistinct; cuticle roughened; gemmae at stem apex or on margins of upper leaves, spherical or oval, unicellular, rarely in branching threads; dioicous; perianth oblong or obovate, truncate; mouth denticulate or subentire; male and female plants mixed together or in separate tufts; male plants slender,

bracts smaller than leaves, lobes nearly equal, dorsal lobe often with a tooth at base; antheridia 2-6, sometimes with short capillary or leaf-like paraphyses.

On moist rocks. Observatory Inlet (38); North Bend (Frye), 1926.

Oregon (1).

Idaho: Moscow Mountain (Clark), 1923.

7. *Scapania umbrosa* (Schrader) Dumortier.

Plants yellow or yellowish green or brown or reddish purple, in closely appressed loose or compact mats; stems 5-15 mm long, erect or ascending, sparingly branched or subsimple, decurved at the apex especially on drying; rhizoids few, colorless, long; leaves transversely inserted, distant to subimbricate, of same size thruout, not decurrent, complicate-bilobed for $\frac{2}{3}$ their length; keel acute or rounded, sometimes with a trace of a wing; dorsal lobe appressed-imbricate except in sterile forms, nearly parallel to stem, ovate, .56-.7 mm long, .5-.58 mm broad, often narrowly pointed, dentate, acute; ventral lobe ovate or oblong-ovate, .86-1.12 mm long, .53-.77 mm broad, 2-3 times as large as dorsal lobe, acute or obtuse or sub-acuminate in slender sterile forms, irregularly serrate-dentate, apex deflexed or somewhat secund; leaf cells orbicular to oval, median 12-30 μ , at base elongated; walls thick; trigones small and indistinct; cuticle minutely granulate; gemmae in dark-brown clusters at apex of stem, oblong-elliptic; dioicous; archegonial inflorescence terminal on main stem; bracts similar to leaves but more equally bilobed and less dentate; perianth twice as long as bracts, reddish purple at base, oblong from an obconic base, compressed; androecium terminal; bracts several pairs, small, saccate, sub-equally lobed; antheridia 1-3 in axils of bracts paraphyses few, short, multicellular; capsule long exserted, oblong-ovate, dark brown; spores brown, 10-12 μ , punctate.

On logs in damp woods. Cascade Mountains (Allen), 1900; Seattle (Frye), 1904; Renton (Frye), 1904; Olympic Mountains (Frye), 1907; Suiattle Basin in Glacier Peak region (Winona Bailey), 1910; Tacoma (Flett), year (?); Gate (Foster), 1912; Friday Harbor (Clark), 1923; north side of Orcas Island (Clark), 1925.

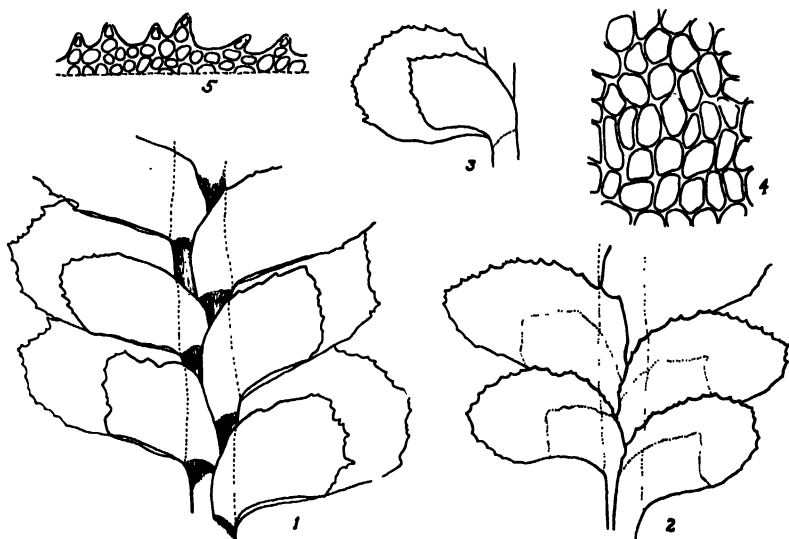
Oregon: Powers Creek (Foster), 1910.

8. *Scapania evansii* Bryhn, Bryologist 4:45. 1901.

Plants more or less tinged with red or reddish brown, densely caespitose; stems 1.5-3 cm long, .1-.3 mm broad, erect and simple; rhizoids few, colorless; leaves transversely inserted, subimbricate to imbricate, stiff, not arching over the stem, complicate-bilobed for $\frac{1}{2}$

their length; keel with a wing 1-2 cells wide, entire or sometimes toothed; dorsal lobe obliquely ovate to suborbicular, .4-.65 mm long, .37-.5 mm broad, acute or sometimes obtuse, dentate, teeth finer than on ventral lobe; ventral lobe obliquely oblong or ovate, broadest a little above the middle, .5-.7 mm long, slightly convex, a little decurrent, twice as large as dorsal, irregularly coarsely dentate, apex rounded; leaf cells rotund or hexagonal; median cells 24-32 μ ; marginal cells smaller and walls twice as thick as in median; cell-walls containing brown pigment; trigones distinct, triangular; cuticle papillate, papillae varying in number with size of cell; archegonial inflorescence terminal; bracts similar to leaves but larger; perianth oblong, entire or dentate; mature capsule lacking.

On damp rocks. Near Humes Glacier in Queets River valley in Olympic Mountains, altitude 5000 feet (Frye), 1907 (reported as *S. intermedia*).



Scapania evansii. 1. Part of plant, dorsal view, $\times 27.5$. 2. Part of plant, ventral view, $\times 27.5$. 3. Leaf, dorsal view, $\times 27.5$. 4. Median leaf cells of ventral lobe, $\times 178$. 5. Margin of ventral lobe, $\times 135$.

Idaho: Bonners Ferry (Frye), 1928.

Montana: Libby (Frye), 1928.

9. *Scapania irrigua* (Nees) Dumortier.

Plants small, yellowish green, rarely brownish; stems 2-5 cm long, flexuose, ascending, simple or sparingly branched; rhizoids rather scarce but extending to the stem tip; leaves rather flaccid, thin,

approximate, or imbricate near the stem tip, embracing the stem, bilobed for half their length into unequal lobes; dorsal lobe convex, loosely incumbent, or erect-spreading with the tip incurved, slightly or not crossing the stem, usually not or hardly decurrent, cordate-triangular or subreniform-triangular, acutely pointed or apiculate, the margin entire or rarely subdentate near the apex of the uppermost leaves; ventral lobe twice as large as the dorsal, frequently undulate, broadly oblong-obovate to subrotund-obovate, apiculate, shortly decurrent, the ventral margin and occasionally the whole lobe reflexed; margin entire or sometimes remotely subdentate near the apex; keel variable, usually only slightly curved, sometimes winged; leaf cells 19-24 μ , roundish-polygonal to roundish-quadrate, translucent, slightly smaller at the margin; walls thin; trigones small but distinct; cuticle granular-punctate; gemmae in clusters at the tips and margins of the uppermost leaves, greenish yellow, elliptical or oval, 2-celled; dioicous; female involucre bracts slightly larger than the leaves; perianth scarcely twice as long as wide, oblong-oval, sometimes plicate above; mouth truncate, dentate or entire; male inflorescence at the tip or middle of the stem; bracts 3-4 pairs, smaller than the leaves, ventricose; antheridia 2-4, broadly oval, on a stalk of about equal length; capsule oval, its inner wall with semiannular thickenings; spores 9-12 μ , brown, granular.

Oregon: Mt. Hood (41). We have not seen this material, and surmise it may be an error in determination.

10. *Scapania curta* (Martius) Dumortier.

Plants bright or dark green, sometimes tinged with brown or with red, in loose inconspicuous mats; stems ascending, 5-15 mm long, thick, simple or innovating below the perianth; rhizoids numerous, colorless, long; leaves transversely inserted, soft, a little larger toward stem apex, complicate-bilobed to middle; keel outwardly rounded or acute, very rarely with trace of wing; dorsal lobe .7-1 mm long, .7-.78 mm broad, triangular-ovate to oblong-ovate, erect to horizontal, appressed-imbricate to spreading, acute, dentate or entire, ascending, a little concave; ventral lobe 1-1.7 mm long, .56-.78 mm broad, orbicular-ovate to obovate, slightly or not at all decurrent, a little concave, flat, acute or obtuse or rarely apiculate, slightly dentate or entire, spreading horizontally; leaf cells hexagonal or round-oval 12-36 μ ; basal cells oblong; walls thin to mediumly thick, pellucid or pigmented; trigones small; cuticle slightly roughened with numerous delicate papillae; gemmae borne in clusters at stem apex or on leaf-

margins, colorless or brown, ovoid or oblong-ellipsoid, 1-2-celled; dioicous; archegonial inflorescence terminal on main stem; bracts similar to leaves; perianth oblong-obovate, 1.5-3.5 mm long, 1-1.8 mm broad, about twice as long as broad, exserted; mouth truncate, ciliate-dentate, very rarely repand; androecium terminal; bracts concave, smaller than leaves; lobes obtuse; capsule oval, dark brown; spores brown, rough, 9-12 μ .

On logs. Near Humes Glacier in Queets River valley (Frye), 1907; Olga (Clark), 1925.

Oregon: Mt. Hood (31).

Wyoming: Craig's Pass and Mt. Washburn, both in Yellowstone National Park (Frye), 1925.

11. **Scapania uliginosa** (Swartz) Dumortier.

Plants in reddish brown to purple or dark green tufts, large; stems erect or ascending, rather flaccid, black or reddish brown, 5-10 cm, leaves destroyed below, simple or sometimes sparingly branched; rhizoids scarce; leaves approximate to imbricate above, flaccid when moist, crisped when dry, bilobed to 1/2-2/3 their length; dorsal lobe reniform, strongly convex, incumbent, scarcely crossing the stem except upper leaves, decurrent; ventral lobe 3-4 times as large, suborbicular, undulate, entire thruout, long decurrent, upper margin strongly reflexed; keel short, strongly curved, winged; cells 20-30 μ , 5-6-angled; walls purple, slightly thickened; marginal cells smaller, subquadrate; walls equally and slightly thickened; trigones minute or absent; cuticle smooth or granular punctate; bracts slightly larger than leaves, more or less equally bilobed, margins entire; perianth long exserted, sometimes not perfectly formed, oblong-obovate, truncate; mouth sinuate-entire or denticulate.

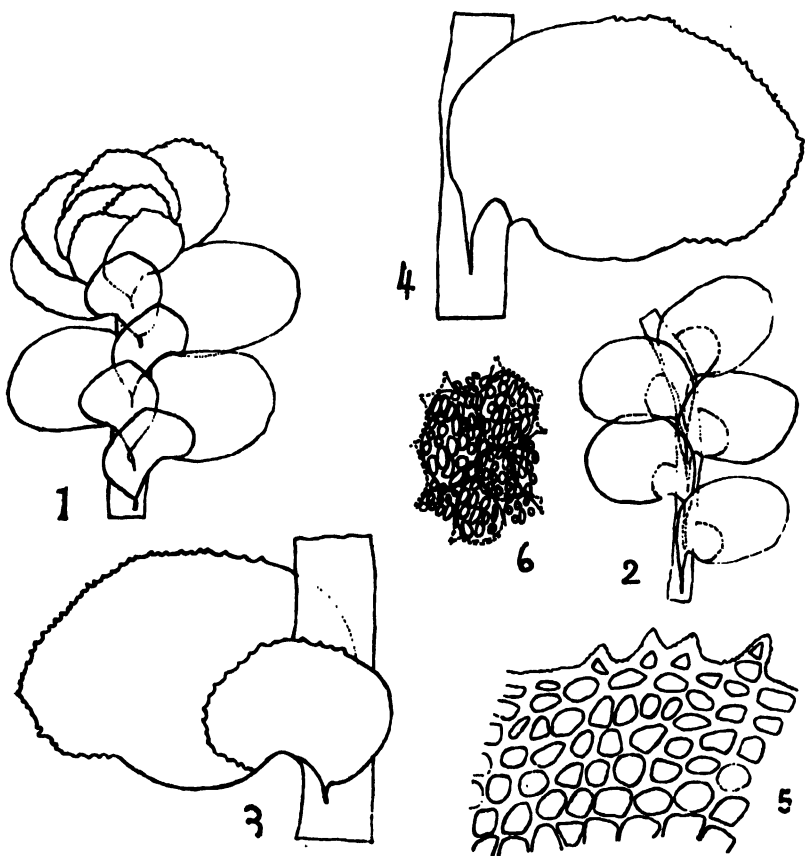
On marshy ground. Darrington (Frye), 1928. O. D. Allen found it on Mt. Rainier but we do not have the data for his material. Dr. A. W. Evans, in a letter referring to the plants says "It is possible that they belong to *S. obliqua* instead of *S. uliginosa*." *S. uliginosa* has the dorsal leaf lobes reniform, hardly crossing the stem, and about half the size of the ventral lobes; *S. obliqua* has the dorsal leaf lobes rather broadly ovate, widely crossing the stem, and 1/3-1/4 the size on the ventral lobes. *S. uliginosa* has also been reported from British Columbia (33) and Colorado (16).

12. **Scapania cordifolia** C. Mueller, Bull. Herb. Boiss. 1903:38. 1903.

Scapania paludosa papillosa Clark. Bull. Torrey Bot. Club 36:306. 1909.

Plants reddish brown to black, in loose mats; stems 3-9 cm long,

3-5 mm wide, erect, simple or dichotomous; rhizoids none or few, colorless; leaves approximate to subimbricate, transversely inserted, 3-4 mm long, 2-3 mm broad, not changing in size toward apex, arching over stem; dorsal lobe obovate to ovate, erect or appressed, obtuse or rarely acute, decurrent, forming a continuous dark line along middle of stem, finely denticulate; ventral lobe 3-4 times size of dorsal lobe, broadly ovate to orbicular, spreading horizontally, not arching over the stem, not decurrent, obtuse or round, finely dentate, teeth .5-1.5 cells long; leaf cells subquadrate to subrotund; marginal cells smaller, 25-30 μ , thicker walled; basal cells elongated; median cells 20-45 μ , walls very thick; trigones small and indistinct except at margin; cuti-



Scapania cordifolia. 1. Part of plant, dorsal view, $\times 18.5$. 2. Part of plant, ventral view, $\times 18.5$. 3. Dorsal view of leaf, $\times 44$. 4. Ventral view of leaf, $\times 44$. 5. Cells from margin of ventral lobe, $\times 314$. 6. Cells from median region of ventral lobe, showing papillae, $\times 314$.

cle roughened with verruculae on both surfaces; verruculae circular to elliptic, 4-10 μ long, about 4 μ broad at center of lobe, becoming smaller toward margin, densely crowded, some large cells showing as many as 25 on each surface; inflorescence wanting.

On wet rocks. Near Humes Glacier in Queets River valley (Frye), 1907; Paradise Valley on Mt. Rainier (Foster), 1909.

Oregon: Newport (Daugherty), 1921.

RADULA

Plants medium in size or rarely small or slender, green or yellowish-green, tinging the water a yellowish green when soaked, prostrate, forming wide depressed mats; stems loosely pinnate or bipinnate, very rarely dichotomous, branches arising laterally from between leaves; rhizoids arising from mammilliform pockets of ventral base of leaf lobes; leaves alternate, incubous, conduplicate-bilobed, the lobes entire; ventral lobe smaller, somewhat inflated near fold, outer margin appressed to dorsal lobe; leaf cells small, often containing oil bodies; underleaves wanting thruout; dioicous or autoicous or paroicous; archegonial inflorescence rarely cladogenous, mature perianth sometimes falsely lateral thru subfloral innovations; bracts a single pair, smaller than the leaves, enlarged ventral base without rhizoids; perianth compressed dorsiventrally, rarely nearly round-carinate or plicate, somewhat bilabiate, truncate; lobes entire or repand-crenate; androecium sometimes ament-like, usually terminal on main stem or branch; bracts 3-35 pairs; lobes subequal; antheridia single, rarely 2-3; calyptra firm and subopaque, wall of 2-3 layers of cells; capsule generally oval-cylindric, 2-3 times as long as broad, dehiscing to base by 4 valves; valves bistratose, outer cells with nodular thickenings, inner cells with delicate transverse striae; seta short, stout; spores large, subglobose or elliptic, minutely granulate or subechinulate-papillate; elaters long, slender, obtuse, closely spiral.

- A. Dorsal leaf lobe obovate, its inner margin adnate to the stem and not arching beyond it; leaves ascending; leaf cells 9-16 μ long. 1. *R. bolanderi*
- AA. Dorsal leaf lobe ovate or quadrate-orbicular, its inner margin not adnate to the stem and arching beyond it; leaves widely spreading; leaf cells 15-24 μ long.
- B. Rhizoids none; gemmae none; plants dioicous. 2. *R. polyclada*
- BB. Rhizoids present; gemmae fairly common; plants paroicous. 3. *R. complanata*

Comparison of species of <i>Radula</i>	1. bolanderi	2. poly-clada	3. com-planata
Inner margin of dorsal leaf-lobe adnate to stem.....	+	—	—
Inner margin of dorsal lobe arching beyond stem.....	—	+	+
Leaves widely spreading or ascending.....	a	s	s
Dorsal lobe quadrate-orbicular, obovate, ovate°	b	v	q
Length of leaf cells in mu.....	9-16	15-22	16-24
Rhizoids present.....	+	—	+
Gemmae present.....	—	—	+
Paroicous, dioicous.....	d	d	p
Spores in mu.....	48-60		36-38

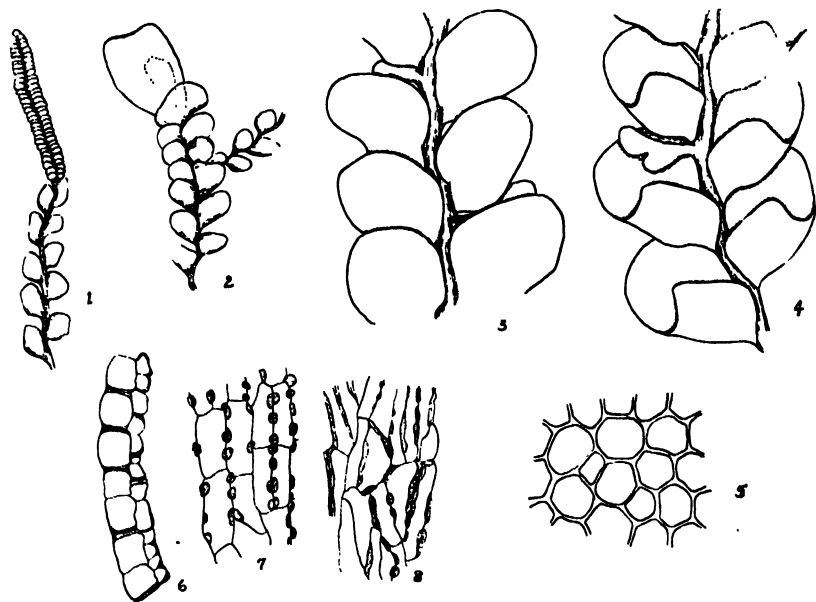
1. *Radula bolanderi* Gottsche Stephani in Hedwigia 23:145. 1884.

Radula spicata Austin, Bull. Torrey Bot. Club 6:19, 1875. Not *Radula spicata* Mitten, Bonplandia 10:19, 1862.

Plants light green, slender, prostrate, forming wide depressed mats; stems 1-2 cm long, pinnate or bipinnate, branches short; leaves touching each other or imbricate, spreading or erect-spreading or somewhat ascending; keel obtuse, arcuate, decurrent; dorsal lobe obovate, .28-.85 mm long, .16-.55 mm wide, plane or slightly concave, very obliquely attached to stem; ventral lobes at first subequal to dorsal, later $\frac{1}{3}$ - $\frac{1}{2}$ as large, rhomboidal-ovate, inflated, subacute or obtuse, appressed to dorsal, inner margin adnate to stem and not incumbent, outer margin obliquely truncate; leaf cells round, 9-16 μ ; walls thin; trigones small, sometimes indistinct; dioicous; archegonial inflorescence terminal; bracts 1 pair; lobes subequal, otherwise similar to leaves; perianth obconic, 1-2.2 mm long, .7-1.2 mm broad, bilabiate, lips entire; androecia terminal on main stem or branch, numerous, linear, spike-like; bracts 10-35 pairs, equally lobed, very closely imbricate, ventricose; capsule brown, oval, cylindric; valves 1 mm long; striae of inner layer indistinct or wanting; spores subglobose or elliptic, 48-60 μ long, densely and minutely echinulate-papillate; elaters .15-.2 mm long, 6-8 μ wide.

On tree trunks. Seattle (Piper), 1891; Seattle (Frye), 1904; Friday Harbor (Frye), 1905; Cathlamet (Foster), 1907; Elwha River valley (Frye), 1907; Aberdeen (Foster), 1909; Renton (Foster), 1911; Seattle (Foster), 1912; Gate (Foster), 1912; Seattle (Foster), 1913; Ronald (Foster), 1913.

Oregon: Salem (2) as *R. spicata*; Mt. Hood Post Office (30); Salem, Silverton, North Silver Creek in Marion County, Forest Grove, Portland, (6); Powers Creek (Foster), 1910; Hult (Foster), 1910.



Radula bolanderi. 1. Part of male plant, dorsal view, $\times 11.5$. 2. Part of female plant, dorsal view, $\times 10$. 3. Part of plant, dorsal view, $\times 27.5$. 4. Part of plant, ventral view, $\times 27.5$. 5. Cells from near leaf tip, $\times 352$. 6. Cross section of capsule wall, $\times 225$. 7. Outer layer of capsule wall, $\times 225$. 8. Inner layer of capsule wall, $\times 225$. (6, 7, 8 after Castle).

2. ***Radula polyclada*** Evans, Bull. Torrey Bot. Club 41:607. 1915.

Plants dull, yellowish green, becoming brown with age, 2-3 cm in length, prostrate in loose mats; stems .2 mm in width, profusely and regularly pinnately branched; branches .1 mm in width, arising almost uniformly behind every leaf, spreading at an angle at 90° , 4-8 mm in length, frequently bearing very short axes of the second order; stem leaves entire, somewhat imbricate, widely spreading at an angle of 70° - 80° , slightly falcate, the keel slightly arched; dorsal lobes of the stem leaves .95 by .65 mm, broadly ovate, convex and often revolute at tip, the apex broadly rounded, the base slightly auriculate and free for $\frac{1}{3}$ the distance, arching only slightly over the stem, only slightly decurrent; ventral lobe .4 by .35 mm, quadrate, appressed to the dorsal lobe, the base free about $\frac{1}{2}$ its length, the free portion slightly auriculate at the point of fusion and arching

only slightly over the stem, the free margin parallel to the keel, the apex obtusely angled; rhizoids entirely lacking; leaf cells plain, without definite trigones, occasionally somewhat thickened at the angles, the cuticle smooth, marginal cells 15 by 10 μ , median cells 22 by 17 μ , basal cells 30 by 25 μ ; leaves of the primary axis more or less imbricate; dorsal lobe .45 by .35 mm, ovate, convex, less widely spreading than the stem leaves; the ventral lobe .2 by .1 mm, subquadrate, the free margin shorter than the keel; leaves of the secondary axes still less widely spreading, subequally bilobed; dioicous; female inflorescence terminal on a short branch of the first order, innovating at the base, the innovations 2, more rarely 1, and not fertile; female bracts large and widely spreading, the keel incurved; dorsal lobe 1.4 by .8 mm, narrowly ovate, rounded at apex, somewhat convex; ventral lobe .85 by .65 mm, rounded at apex, somewhat concave; perianth, male inflorescence and sporophyte unknown. Adapted from Castle (6).

Near Olympic Hot Springs (Foster), 1914.

Its range is from Washington to Alaska, and it is apparently more common north of our area.



Radula polyclada. 1. Part of plant, ventral view, $\times 12.5$. 2. Median leaf cells, $\times 330$. (After Evans).

3. *Radula complanata* (Linne) Dumortier.

Plants yellowish green, somewhat flaccid, prostrate, forming closely depressed mats; stems 1-6 cm long, irregularly pinnate or bipinnate; rhizoids short, colorless; leaves closely imbricate, spreading; dorsal lobe oval to suborbicular, .5-1.6 mm long, .4-1.4 mm wide, ventrally concave; apex obtuse, deflexed or nearly plane; inner margin not adnate to stem, arching beyond it; keel strongly arcuate; ventral lobe nearly $\frac{1}{4}$ the size of dorsal, subquadrate or quadrate or rarely oblong, elongated in direction of keel, appressed to dorsal lobe

or inflated at base, obtuse or acute; leaf cells round, 16-24 μ ; walls thin; trigones small; gemmae sometimes present on leaf margins, discoid, usually multicellular, with chloroplasts and oil bodies; parocious; archegonial inflorescence terminal on main stem or short branch; bracts 2-3 pairs; lobes subequal or the ventral $\frac{1}{2}$ as large as the dorsal, obtuse; perianth obconic or elongated-obconic, 1.8-2.8 mm long, .9-1.12 mm wide, strongly compressed, bilabiate, lips entire or slightly repand; androecium typical; capsule elliptic or obovoid, .9-1.3 mm long, .45-.55 mm wide, exserted; seta 1-2 mm long; spores subglobose, 30-38 μ , finely granulate-papillate; elaters .16-.21 mm long, 6-9 μ thick.

On tree trunks. Common about Puget Sound. Seattle (Piper), 1891; Cascade Mountains (Allen), 1900; Roy (Allen), 1901; Seattle (Frye), 1904; Roche Harbor (Frye), 1905; Friday Harbor (Frye), 1905; Cathlamet (Foster), 1907; near Humes Glacier in Queets River valley (Frye), 1907; Camp Elkhorn in Elwha River valley (Frye), 1907; Renton (Foster), 1911; Seattle (Foster), 1911; Dungeness (Foster), 1913; Friday Harbor (Clark), 1923; Orcas Island (Clark), 1925; Camas (Frye), 1925; Darrington (Frye), 1928.

Oregon: Salem (2) as *R. hallii*; Mt. Hood (31); Albany (Van Wert), about 1923.

Idaho (2).

Montana: Avalanch Basin, Lake McDonald, Holzinger Basin, (40); Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928; Whitefish (Frye), 1928.

MADOTHECA (Porella)

Plants large, dark green or yellowish brown, more or less regularly 1-3-pinnate or rarely subsimple; rhizoids usually few, in tufts at base of underleaves; leaves incubous, alternate, distant to closely imbricate, deeply 2-cleft; dorsal lobes distant to imbricate, obliquely ovate, suborbicular to oblong-ovate, obtuse or rounded, entire or repand or more or less dentate; ventral lobe smaller than dorsal, ovate or linguliform or oblong or linear; margin entire or toothed, plane or revolute; underleaves present thruout, lingulate, oblong or linear, entire or toothed, base at both sides often long-decurrent; leaf cells medium in size, in our species with trigones; archegonial inflorescence terminal on short lateral branch; archegonia numerous; bracts 1-2 pairs, with single bracteole and underleaf at base of branch; this underleaf either united with stem leaf to make ventral lobe, or else free and thus leaving stem leaf unlobed; perianth obovate or oval, com-

pressed dorsi-ventrally toward upper part, exserted, base obconic; mouth entire or ciliate or dentate; androecium terminal, oblong or in spikes; antheridia single; capsule spherical to ovoid-oblong, short-stalked, yellowish brown, dehiscing nearly to base by unequal rigid valves; cell walls mostly with nodulose thickenings; spores broader than elaters, echinate; elaters with 2 spirals.

Comparison of species of <i>Madotheca</i> and <i>Lejeunea</i>	Madotheca				<i>Lejeunea</i> <i>cavifolia</i> , p. 163
	1. platy- phylla	2. roellii	3. eudeana	4. navicularis	
Underleaves bilobed.....	—	—	—	—	+
Underleaves long decurrent.....	+	+	+	+	+
Dioicous, autoicous.....	d	d	d	d	a
Perianth somewhat 3-angled or distinctly 5-angled.....	3	3	3	3	5
Trigones, large, small, minute.....	s	s	m	l	m
Trigones bulging into the cells.....	—	—	—	+	—
Ventral leaf-lobe about half the width of the underleaves, less than half, about the same..	h	h	l	s	h
Underleaves distant, imbricate.....	i	i	d	i	d
Ventral leaf-lobe long decurrent.....	—	—	+	—	—
Ventral lobe with outer margin broadly reflexed	—	—	+	—	—
Cell-hollow round-polygonal, rounded.....	r	r	p	r	p
Dorsal leaf-lobe obtuse, rounded, truncate....	r	t-o	r	r-o	r
Plants usually dull or usually shining.....	d	s	s	s	
Underleaves subdentate, entire, or with few teeth at extreme base.....	e-f	s	e-f	e	e
Perianth-tip bilabiate, truncate, rounded.....	b	t	b	b	t-r
Perianth gobletshaped, obovate, oval.....	v	b-g	v	b	v
Mouth of perianth repand-lobate, 5-lobed, denticulate, crenulate, ciliate.....	d-l	d	r	ld-nd	5
Ventral leaf-lobe entire, dentate.....	e-d	e-d	c	c	d

A. Trigones not bulging into the cells, small; ventral leaf lobes about half as large as the underleaves or less.

B. Ventral lobe about half as wide as the underleaf, not long decurrent, its outer margin narrowly reflexed if at all; underleaves imbricate.

C. Plants usually dull; dorsal lobe rounded at tip; perianth oval, bilobed.

1. *M. platyphylla*

CC. Plants usually shining; dorsal lobe truncate to obtuse; perianth broadly obovate or gobletshaped, truncate.

2. *M. roellii*

- BB. Ventral lobe less than half as wide as the underleaf, long decurrent, its outer margin broadly reflexed; underleaves distant.

3. *M. cordeana*

- AA. Trigones bulging into the cells in older leaves, large; ventral leaf lobes about the same width as the underleaves.

4. *M. navicularis*

1. ***Madotheca platyphylla*** (Linne) Dumortier.

Jungermannia platyphylla Linne, Sp. Pl. 2:1134, 1753.

Jungermannia platyphylloidea Schweinitz, Sp. Fl. Amer. Sept. Crypt. p. 9, 1821.

Madotheca navicularis Nees, Naturgesch. Eur. Leberm. 3:176. 1838.

Porcella thuja Lindberg, Acta Soc. Sci. Fennica 9:337. 1869.

Porcella platyphylla Lindberg, Acta Soc. Sci. Fennica 9:339. 1869.

Plants dull or more rarely with a slight luster, opaque or a little pellucid, yellowish to very dark green, rather rigid, usually in compact mats; stems somewhat regularly or irregularly 1-3 pinnate, 3-8 cm long, procumbent; branches obtuse, very rarely subattenuate; dorsal lobes of leaves rather densely imbricate, appressed, or with the superior margin ascending or slightly reflexed, obliquely ovate to obliquely orbicular-ovate, rounded-obtuse, .85-2.1 mm by .65-1.7 mm, apex more or less decurved, superior margin repand-dentate or subentire, the inferior sometimes a little undulate-cripsed; leaf cells at inferior basal angle scarcely smaller; trigones distinct; ventral lobes somewhat obliquely ovate to oblong, obtuse, rarely subacute, .4-1.2 mm by .25-.85 mm, length about 3/5 the width of the dorsal, nearly equaling underleaves in width or only half as broad; margins recurved, entire or with a single acute tooth at apex, scarcely decurrent, at least the outer one recurved; underleaves approximate or subimbricate, semiorbicular to quadrate-oblong, rounded-obtuse, margin reflexed especially at apex, long-decurrent, sometimes repand or sparingly denticulate at apex but otherwise entire; dioicous; female branch short; dorsal lobes of bracts obtuse, more rarely acute, ventral lobes usually acute, margins of both entire or denticulate; perianth oval, inflated ventrally along median line specially when young, narrowed above; leaves of the perianth denticulate or subciliate, plane or often lightly revolute, specially toward the lateral margins; male spikes oval to oblong, 1.5-3 mm long; capsule oval, light brown, the valves often irregularly split; spores 32-45 μ , echinulate; elaters 180-250 μ long, 7-10 μ thick, 1-2 spiral.

Oregon: Portland (44).

Idaho (4).

Wyoming (4).

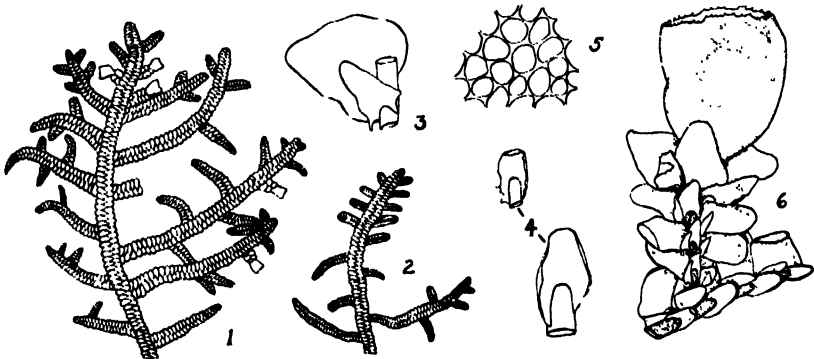
It has also been found near Victoria in British Columbia.

2. **Madotheca roellii** Stephani, Bot. Centralb. 45:203. 1891.

Porella roellii Stephani, Bot. Centralb. 45:203. 1891.

Plants yellowish brown or green, more or less shining; stems 4-8 cm long, simple or dichotomous; dorsal leaf lobe closely imbricate, obliquely ovate, spreading, .85-1.5 mm long, .6-1.5 mm broad; apex more or less truncate or narrowed or obtuse, very rarely apiculate; lower margin more or less undulate-crested, upper margin repand; ventral lobe obliquely ovate or ovate or linguliform, subacute or obtuse, .35-.4 mm long, .16-.21 mm broad, suberect or spreading, scarcely united with dorsal lobe, slightly concave; margin entire, plane or recurved, more or less strongly decurrent, basal margin usually strongly spurred outwardly; spur entire or dentate; leaf cells 18-30 μ , walls mediumly thick thruout; trigones present; cells in wing of dorsal lobe smaller and with distinct trigones; underleaves more or less imbricate, ovate or liguliform, .35-.45 mm long, .3-.35 mm wide, apex rounded or obtuse; margin recurved, entire or rarely subdentate, long decurrent; dioicous; female inflorescence on short or elongated branch; bracts usually 2 pairs, nearly similar to stem-leaves; inmost ones a little larger, subacute, entire or repand-denticulate; bracteole oval, subentire or denticulate; perianth large, broadly ovate or goblet-shaped, ventral side undulate, concave or sometimes inflated, scarcely narrowed toward mouth, not lobed; mouth denticulate or slightly deflexed at side; androecia in spikes, 1-2 mm long; capsules and spores unknown.

On moist stony cliffs or on stones at water's edge. Lake Kechelus (Roell), 1888; Olympia (Henderson), 1895; Upper Valley of the



Madotheca roellii. 1. Part of female plant, $\times 1$. 2. Part of male plant, $\times 1$. 3. Leaf from stem, showing ventral lobe, $\times 11.5$. 4. Underleaves, $\times 11.5$. 5. Leaf cells, $\times 152$. 6. Female branch with mature perianth, $\times 6$. (After Howe).

Nisqually (Allen), 1905; Westport (Foster), 1908; Friday Harbor (Clark), 1923; Orcas Island (Clark), 1925; Camas (Frye), 1925; Joyce (Frye), 1927.

Oregon: Portland, Oregon City, Bridal Veil Falls, (31); Maplewood (Van Wert), about 1923.

Idaho: Moscow (Clark), 1924.

Montana: Piegan Pass trail from Many Glaciers in Glacier National Park (Frye), 1928.

3. *Madotheca cordeana* (Huebener) Dumortier.

Plants bright green, prostrate, in loose mats, rather dull, soft, flaccid; stems 3-10 cm long, prostrate or sometimes ascending, pinnate; dorsal lobes of leaves subimbricate to imbricate, oblong-ovate to sub-orbicular-ovate, 1.4-2.3 mm long, 1.5-2.6 mm broad, more or less concave, apex rounded or obtuse, margin entire or denticulate; ventral lobe obliquely ovate, .35-.7 mm long, .12-.4 mm broad; margins revolute giving the lobe the appearance of being twisted, dentate or subciliate at base or sometimes with 1 tooth on outer margin; underleaves distant, quadrate-orbicular or ovate, .98-1.5 mm long, repand-undulate, base long-decurrent; wing usually acutely dentate or ciliate; leaf cells round, 27-45 μ ; trigones present but small; dioicous; archegonial inflorescence terminal on a short branch; bracts, 1 pair; ventral lobe acute or subobtuse, margin repand; dorsal lobe obtuse; bracteole linguliform, entire; perianth ovate, lateral margin deflexed, deeply bilabiate, lobes entire or repand or dentate; androecia in spikes 1-2.5 mm long; capsule globose, very short-stalked, wall of 3 layers; inner layers without thickenings; spores 35-49 μ , yellowish green, smooth; elaters 2-3-spiral, brown. Our specimens were without capsules.

On rocks in streams, sometimes on trunks of trees in very moist woods. Hamilton (Foster), 1905; Guemes Island (Frye), 1905; near headwaters of Elwha River in Olympic Mountains (Frye), 1907; Liberty Creek in Spokane County (Bonser), year (?); Seattle (Bolt), 1918; Friday Harbor (Clark), 1923; Orcas Island (Clark), 1923, 1925.

Oregon: Albany (Van Wert), about 1923.

Idaho: Moscow Mountain (Clark), 1923.

Montana: Avalanch Basin, Bigfork, Lake McDonald, Mt. Trilby, (40); Iceberg Lake and Piegan Pass trails from Many Glaciers in Glacier National Park (Frye), 1928; Whitefish (Frye), 1928.

4. *Madotheca navicularis* (Lehmann and Lindenberg) Dumortier, Rec. d'Observ. p. 27. 1835.

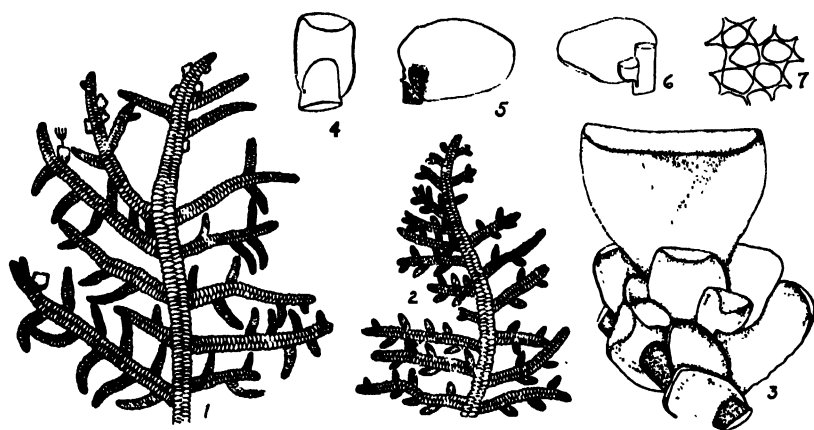
Jungermannia navicularis Lehmann and Lindenberg, in Lehmann Pugill 6:38. 1834.

Madotheca douglasii Taylor, London Jour. Bot. 5:379. 1846.

Madotheca recondita Lehmann and Lindenberg, in Nees Syn. Hep. p. 274. 1844-1847.

Porella navicularis Lindberg, Acta Soc. Sci. Fennica 9:337. 1869.

Plants glossy, yellowish or brown or green, in thick mats; stems 5-10 cm long, prostrate, 1-2-pinnate, ascending at apex on drying, concave and somewhat deflexed; leaves alternate, at right angles to stem; dorsal lobe ovate to orbicular-ovate, 1.3-2.4 mm long, 1.1-1.3 mm broad, appressed, on drying more or less wrapped about the stem; margin entire or slightly repand, lower basal margin undulate-cripsed, upper margin often lacerate-cripsed, decurrent; apex rounded or obtuse, decurved; ventral lobe oval, .4-1 mm long, .33-.7 mm wide, obtuse; margin entire, decurved, base rounded outwardly; leaf cells rotund to polygonal, 27-36 μ , basal inferior angle of dorsal lobe composed of small and very thick-walled cells 10-15 μ ; trigones large, triangular; underleaves approximate, quadrate-oblong; apex rounded or obtuse, sometimes deflexed; margin entire, long decurrent; dioicous; female inflorescence terminal on very short stem; bracts 1 pair; dorsal lobe very obtuse, ventral lobe sparingly dentate or entire; bracteoles broad, entire; perianth broadly obovate from an obconic base, dorsiventrally compressed, not narrowed; mouth deeply bilabiate; lobes



Madotheca navicularis. 1. Part of female plant, $\times 1$. 2. Part of male plant, $\times 1$. 3. Female branch with young perianth, ventral view, $\times 10.5$. 4. Underleaf, $\times 11.5$. 5. Leaf, dorsal view, $\times 6$. 6. Leaf, showing ventral lobe, $\times 6$. 7. Leaf cells, $\times 152$. (After Howe).

ciliate or dentate or crenulate or entire; androecium oblong, 1.5-2.5 mm long; antheridia single; capsule ovoid, exserted, yellowish green, .05-.09 mm in diameter, echinulate; elaters with 2-3 spirals, obtuse, .275-.325 mm long, 7-10 μ thick.

On trunks of trees or rarely on rocks: common about Puget Sound. Enumclaw (Roell), 1888; Weston (Roell), 1888; Seattle (Roell), 1888; Seattle (Piper), 1889; Puyallup (Cooler), 1891; Olympia (Henderson), 1892; Tacoma (Flett), 1899; Seattle (Frye), 1904; Roche Harbor (Frye), 1905; Guemes Island (Frye), 1905; Cathlamet (Foster), 1908; Liberty Creek (Bonser), 1907; Westport (Frye); Elwha River valley in Olympic Mountains (Frye), 1907; Bellingham (Romine), 1907; Burlington (Clark), 1911; Kalama (Frye), 1911; Pacific Beach (Foster), 1911; Mount Ellinor (Foster), 1912; Dungeness (Foster), 1913; Friday Harbor (Clark), 1923; Orcas Island (Clark), 1925; Mt. Angeles (Frye), 1927; Beaver (Frye), 1927.

Oregon: Canyonville (Frye), 1922; Wolf Creek (Frye), 1922; Port Orford (Frye), 1922; Bandon (Frye), 1922; Brookings (Frye), 1922; Albany (Van Wert), about 1923.

Idaho: Moscow (Clark), 1924.

LEJEUNEA

Plants small or mediumly large, pinnate or irregularly branched; leaves imbricate or contiguous; dorsal lobe usually widely spreading, ovate to obovate; apex rounded to obtuse; margin entire to crenulate from projecting cells; ventral lobes small, sometimes obsolete, inflated, rarely plane; leaf cells thin walled, transparent, not papillose; underleaves small, rarely half as large as the leaf, roundish, bifid; female inflorescence terminal on a main branch, with 1-2 innovations, bracts almost similar to the leaves; perianth nearly always with 5 acute keels, the keels smooth or nearly so; male inflorescence nearly always on a short lateral branch.

1. *Lejeunea cavifolia* (Ehrhart) Lindberg.

Compared with *Madotheca* on page 158.

Plants in yellowish green to green patches; stems 1-2 cm long, prostrate, irregularly much branched; rhizoids scarce, at base of underleaves; leaves imbricate, spreading to erect-spreading; dorsal lobe slightly convex or flat, about 5 times as large as the ventral, crossing the stem, ovate to oval, apex rounded or broadly obtuse; margin entire; ventral lobe strongly inflated, ovate; margin involute, with an

obtuse 1-celled tooth at the free angle; leaf cells 5-7-angled, 22-35 μ , walls thin but frequently with small intermediate thickenings; trigones usually minute; cuticle smooth; underleaves distant, subappressed, oval-rotund, narrowed at base, not decurrent, equaling or exceeding the ventral lobe, bilobed to the middle; sinus usually obtuse; lobes obtuse to subacute, entire or nearly so; autoicous; female inflorescence on a long or a short branch, usually with a single innovation; bracts unequally complicate-bilobed; dorsal lobe narrowly and obliquely oblong-obovate, obtuse or subacute, entire; ventral lobe much smaller, linear-oblong to lanceolate; perianth about half exserted, oval-oblong from a narrow base, rounded or truncate at apex, sharply 5-angled above, the angles smooth or sometimes slightly crenulate, the beak short; male inflorescence on a short branch; bracts in 2-4 pairs, ventricose, slightly and nearly equally bilobed, the lobes rounded; antheridia in pairs; capsule globose; spores 28-43 μ long, usually irregularly linear-oblong but some oblong, sometimes angular, greenish brown, densely and coarsely papillose.

Oregon: Portland (44).

We have not seen the material, and know of no other collection of it within our area other than that above reported by Pearson.

FRULLANIA

Plants large or small, depressed-caespitose, generally reddish brown but sometimes green or black; stems mediumly stout, opaque, of several layers of cells, pinnate; branches lateral, arising from axils of stem-leaves but always free from them; rhizoids arising in tufts from base of underleaves; leaves alternate, somewhat obliquely inserted to nearly transversely, complicate-bilobed; dorsal lobe incubous, obliquely ovate to suborbicular, entire; ventral lobes usually inflated, helmet-shaped, cucullate, cylindric-clavate, rarely reniform, more or less distant from stem, bearing on underside a small or almost subulate or triangular process (stylus); lobule at base of branch subequally bilobed, mostly explanate; leaf cells small to medium; trigones more or less distinct, also with intermediate thickenings; underleaves present thruout, smaller than the stem-leaves, bifid; dioicous or autoicous; archegonial inflorescence on a short stem; bracts 2-5 pairs, larger than leaves, entirely free from perianth; the innermost pair connate with bracteoles and with each other; lobules evolute, subentire, more or less dentate or ciliate or laciniate; perianth free, emersed, more or less compressed dorsi-ventrally, triangular in cross

section, third angle ventral, with or without short supplementary dorsal or ventral ridges or folds, otherwise smooth, contracted at apex to a tubular beak, irregularly ruptured by exsertion of capsule; androecium occupying short lateral branch, globose to oblong; bracts saccate, closely imbricate, subequally bilobed; antheridia 3-4; calyptra free, included, pyriform or obovoid, fleshy; capsule globose, exserted on short stalk, dehiscing to base by 4 straight valves; walls bistratose; elaters few, short, with 1 spiral, persistently affixed to the upper half of the capsule valves, free ends truncate or with a trumpet-like expansion; spores large, papillate or verruculose.

Comparison of species of <i>Frullania</i>	1. bolanderi	2. nisquallensis	3. franciscana	4. californica
Ventral leaf lobe how many times as long as wide.....	1	1.3-1.7	1.3-1.7	1.8-2.5
Flagella present.....	+	—	—	—
Ventral lobe helmetshaped, oval, clavate..	h	c-o	c-o	c-o
Perianth terminal on main stem.....	+	—	—	—
Dorsal lobe rounded-obtuse, acuminate-apiculate, acute.....	r	t	r-m	r
Margin of underleaf plane, slightly recurved, strongly recurved.....	p	t	p	p-l
Underleaves rhombic-ovate, quadrate-orbicular, suborbicular, reniform.....	m-s	s-n	m	q
Ventral lobes once their width, half their width or less from the stem.....	l	o	o	h
Dorsal leaf usually with short medial line of discolored cells, or these scattered, if any.....		s	l	s

A. Flagella present; ventral lobe helmet-shaped, longer than broad; perianth terminal on main stem. 1. *F. bolanderi*

AA. Flagella none; ventral lobe oval to short-clavate, much longer than broad; perianth terminal on short branch.

B. Dorsal lobe acute, acuminate-apiculate; discolored cells scattered or wanting, rarely in a median line; leaf-cells 16-30 μ ; underleaves suborbicular or reniform, auriculate, bifid for $\frac{1}{4}$ their length, margin strongly recurved.

2. *F. nisquallensis*

BB. Dorsal lobe round-obtuse.

C. Dorsal lobe usually with a median row of discolored cells; leaf-cells 16-25 μ ; underleaves subquadrate-rhombic to obovate, gradually narrowed toward base but

sometimes auriculate; their margin with blunt tooth toward middle.

3. *F. franciscana*

CC. Dorsal lobe with discolored cells scattered or wanting; leaf-cells 10-20 μ ; underleaves subquadrate-orbicular, more or less auriculate; their margin entire, plane or slightly reflexed.

4. *F. californica*

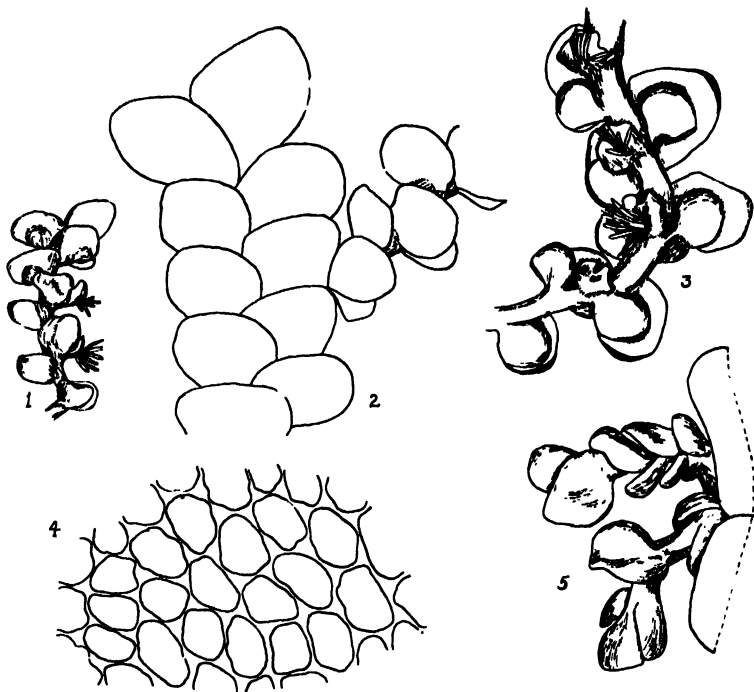
1. ***Frullania bolanderi*** Austin, Proc. Acad. Nat. Sci. Philadelphia 1869:226. 1869.

Frullania petalumensis Gottsche, by Bolander in Calif. Med. Gaz. 1870:184. 1870.
Frullania hallii Austin, Bull. Torrey Bot. Club 6:20. 1875.

Plants dark green to reddish brown, closely appressed, creeping or caespitose; stems 6-20 mm long, irregularly pinnate; branches sometimes prolonged into erect or ascending flagella; flagella crowned with a few slightly developed leaves, generally with horizontal-spreading or subsquarrose underleaves and rudimentary leaves; leaves alternate, obliquely inserted; dorsal lobe subimbricate to imbricate, erect or ascending when moist, ovate or suborbicular, .3-.6 mm long, .27-.45 mm wide, arching over stem; base rarely truncate; margin entire, decurved at apex; apex obtuse or rounded; ventral lobe large, helmet-shaped, .2-.32 mm long, .18-.27 mm broad; base truncate, appressed to stem; stylus small, lanceolate or subulate; median leaf cells of dorsal lobe 8-30 μ ; walls thick; trigones small and indistinct or sometimes very distinct; intermediary thickenings very rare; underleaves distant, obovate or suborbicular, a little wider than the stem, bifid for $\frac{1}{3}$ their length; lobes subacute; margin plane, entire or bearing 1-2 teeth at side; dioicous; archegonial inflorescence terminal on main stem or principal branch; bracts 2-3 pairs, 2-3 times as large as the leaves, unequally bilobed; ventral lobes ovate or lanceolate, obtuse or subacute, plane or slightly concave ventrally, entire except for tooth near center of margin; dorsal lobe round-obtuse, ovate, entire or slightly repand; bracteoles ovate to oblong-ovate, bifid for $\frac{1}{4}$ - $\frac{1}{3}$ their length; lobes and sinuses acute but sometimes rounded or emarginate or rarely 3-4-dentate, connate on both sides; perianth half emersed, obovoid, 1.2-1.5 mm long, .8-1.2 mm wide, with a broad 2-angled keel, also with 1 or more supplementary ridges, rarely with tubercles; the beak short and broad mouth flaring; androecium terminal on short branch, ovoid to oblong; bracts 4-15 pairs, saccate, closely imbricate; antheridia 2-4; capsule globose, exserted; spores variable in size and form, 40-60 μ in greatest diameter.

On bark of living trees. Roy (Allen), 1901; Seattle (Bailey), 1905; (Frye), 1905; Roche Harbor (Frye), 1905; (Foster), 1907; Dungeness (Foster), 1914.

Oregon: Salem (2) as *F. hallii*; Albany (Van Wert), about 1923.

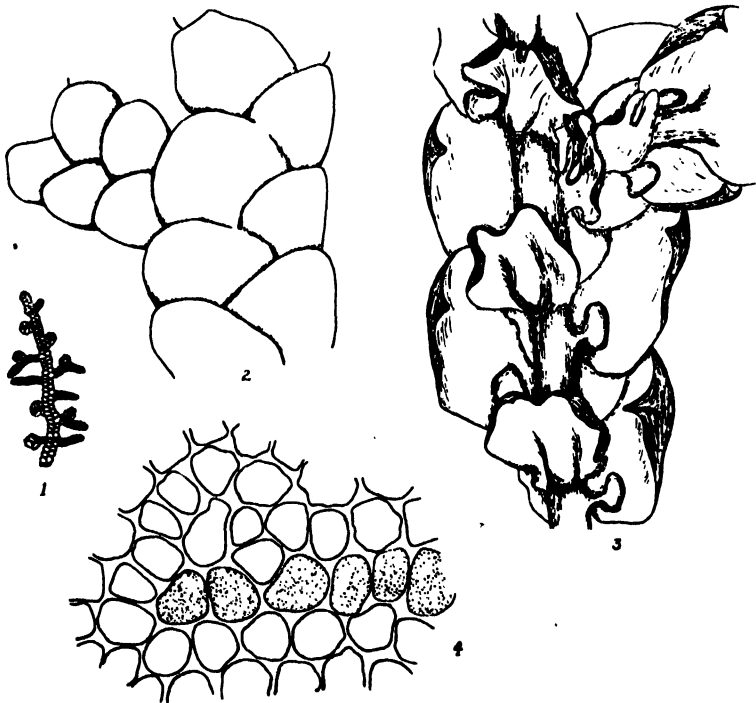


Frullania bolanderi. 1. Part of plant, dorsal view, $\times 10$. 2. Part of plant, dorsal view, $\times 27.5$. 3. Part of plant, ventral view, $\times 27.5$. 4. Median leaf cells from dorsal lobe, $\times 352$. 5. Flagella, dorsal view, $\times 82.5$.

2. ***Frullania nisquallensis*** Sullivant, Mem. Amer. Acad. 2, 4:175. 1849.

Plants reddish brown or yellowish green, depressed-caespitose; stems 1-3 cm long, prostrate thruout, usually bipinnate, without flagella; dorsal leaf-lobes ovate or obliquely ovate, .56-1.2 mm long, .55-.9 mm broad, imbricate, cordate at base, extending beyond stem, entire; apex apiculate or acuminate, decurved; discolored cells scattered, not in a median line; lobules oval-cylindric or short-clavate, .16-.21 mm long, .09-.14 mm wide, separated by less than their own width from stem; stylus minute, subulate; median leaf cells subrotund or subquadrate, 16-30 μ ; walls thick; trigones and intermediary thicken-

ings sometimes conspicuous; underleaves distant to contiguous, sub-orbicular or reniform, $1-3\frac{1}{2}$ times as wide as stem, auriculate at base, bifid for about $\frac{1}{4}$ their length; lobes acute or apiculate, sinus rather broad, obtuse or subacute; margins entire, strongly recurved at least at apex; dioicous; archegonial inflorescence terminal on short branch; bracts 3 pairs, deeply and unequally bifid; dorsal lobe ovate or ovate-lanceolate, entire, sinuous or very sparingly dentate; lobules mostly subulate-acuminate, canaliculate or subtubular by recurving margins, bearing on 1 side toward base a small laciniated segment or a cluster of cilia; inmost bracteoles connate with the bracts on both or sometimes only on 1 side, ovate, bifid for $\frac{1}{3}-\frac{1}{2}$ their length; lobes of bracteoles similar to lobules of bracts, margin ciliate or dentate toward base; perianth long-ovoid, 2-2.5 mm long, .9-1.2 mm wide, gradually narrowing to short beak, strongly 1-keeled ventrally, smooth; androecium ovoid; bracts 4-9 pairs; capsule exserted by its own diameter; spores 60-100 μ in greatest diameter, verruculose.



Frullania nisquallensis. 1. Part of female plant, dorsal view, $\times 2$. 2. Part of plant, dorsal view, $\times 27.5$. 3. Part of female plant, ventral view, $\times 27.5$. 4. Median leaf cells of dorsal lobe, showing central row of discolored cells, $\times 352$.

On rocks and tree trunks. Seattle (Piper), 1891; Olympia (Henderson), 1891; Anacortes (Sears), 1892; Roy (Allen), 1901; Friday Harbor (Frye), 1904; Roche Harbor (Frye), 1905; North Bend (Frye), 1906; Nahcotta (Frye), 1908; South Bend (Frye), 1908; Aberdeen (Foster), 1909; Burlington (Clark), 1910; Pacific Beach (Foster), 1911; Renton (Foster), 1912; Dungeness (Foster), 1913; Chico (Frye), 1915; Granite Falls (Frye), 1921; Tolt (Frye), 1923; Robe (Frye), 1925; Beaver (Frye), 1927.

Oregon: Astoria (45); Rainier (31); Bandon (Frye), 1922; Cape Arago (Frye), 1922.

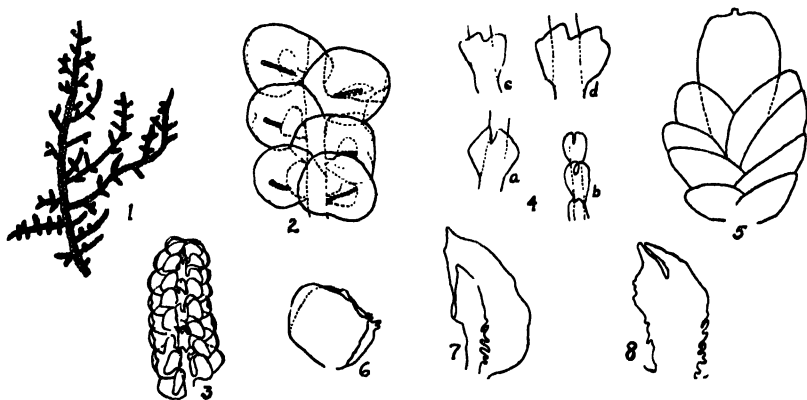
3. *Frullania franciscana* Howe, Erythea 2:99. 1894.

Frullania grayana californica Austin (part), Underwood in Bull. Illinois State Lab. Nat. Hist. 2:67. 1884.

Frullania unciflora californica Gottsche, Bolander in Calif. Med. Gaz. 1870:184. 1870.

Frullania tamarisci Nees (?), Bolander in Calif. Med. Gaz. 1870:184. 1870. Not *F. tamarisci* (Linne) Dumortier.

Plants reddish brown or green, forming depressed mats; stems 1-4 cm long, prostrate, bipinnate; flagella none; leaves alternate; dorsal lobe imbricate, obliquely ovate, .5-1 mm long, .45-.8 mm wide, entire; base cordate, wider than stem; apex round or obtuse or apiculate or acuminate, decurved, with 1-2 rows of discolored cells in median parts; ventral lobe oval-cylindric to short clavate, .1-.2 mm long, .08-.13 mm wide, separated from stem by its own width;



Frullania franciscana. 1. Female plant, $\times 1$. 2. Part of plant, dorsal view, showing location of row of red cells in upper lobe, $\times 19$. 3. Branchlet, ventral view, $\times 17$. 4. Various forms of underleaves; (a) normal, (b) from ultimate branchlet, (c, d) other forms, $\times 17$. 5. Perianth and surrounding bracts, dorsal view, $\times 13$. 6. Leaf from below the bracts, $\times 16.5$. 7. Bract, $\times 17.5$. 8. Bracteole, $\times 17.5$. (After Howe).

stylus minute; underleaves distant, obovate-orbicular, usually rhombic-ovate, 2-2½ times broader than stem, gradually narrowed to base, either appendiculate or auriculate at base, bilobed for ⅓ their length; lobes obtuse; sinus acute; margin entire with 1 tooth near middle; leaf cells rotund to subquadrate, 10-24 μ ; walls thick; trigones and intermediate thickenings conspicuous toward base; dioicous; archegonial inflorescence terminal on short branch; bracts 2-3 pairs, usually bilobed; lobes of inmost pair ovate, acute or apiculate or rarely obtuse, dorsal base ciliate, otherwise entire; lobules ovate or lanceolate, slightly concave ventrally, acute, ciliate at ventral margin; bracteoles connate at 1 side with bracts, ovate, bilobed to their middle; lobes of bracteoles lanceolate, sinus narrow, ciliate at base; perianth oblong-obovate, 1.1-2.3 mm long, .8-1.1 mm broad, abruptly contracted at mouth, strongly 1-keeled, ventrally smooth; androecium subglobose; bracts 3-7 pairs; antheridia 3; capsule exserted; spores 60-80 μ , roughened in small circular patches.

On tree trunks and rarely on rocks. Roche Harbor (Frye), 1907; Westport (Foster), 1908; Ilwaco (Frye), 1908; Kalama (Frye), 1911; Friday Harbor (Clark), 1923; La Push (Frye), 1927.

Oregon: Powers Creek (Foster), 1910; Portland (Flinn), 1912.

4. ***Frullania californica*** (Austin) Evans, Trans. Connecticut Acad. 10:25. 1897.

Frullania grayana californica Austin (part), Underwood in Bull. Illinois State Lab. Nat. Hist. 2:67. 1884.

Frullania asagrayana californica Austin, Howe in Erythea 2:98. 1894.

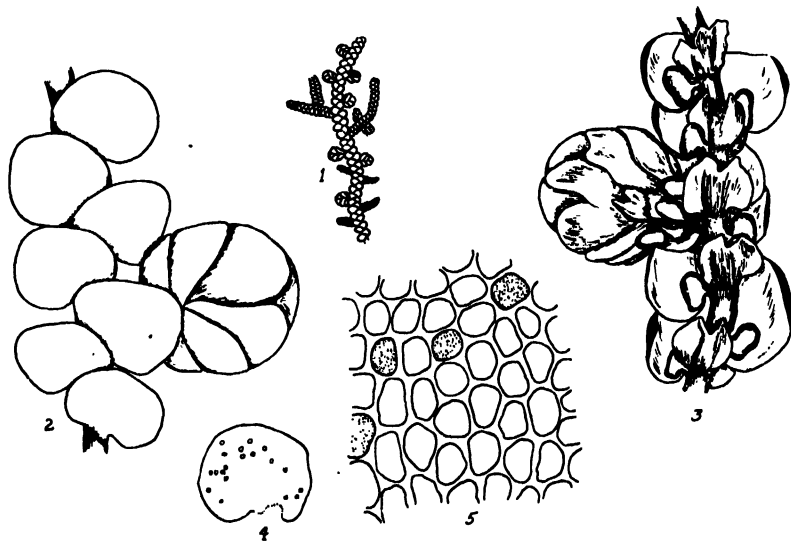
Frullania asagrayana alsophila Howe, Erythea 2:99. 1894.

Plants reddish brown to yellowish green, depressed-caespitose; stems 1-5 cm long, prostrate, 1-2-pinnate; rhizoids colorless, short; dorsal leaf-lobes imbricate, suborbicular, .4-7 mm long, arching beyond stem, cordate at base, entire; apex rounded, slightly decurved; discolored cells wanting or rarely scattered, never in a median row; ventral lobe oval or shortly clavate, .14-.22 mm long, 5-13 μ broad, separated from stem by half its width; stylus disc-like, subulate, minute; underleaves approximate or distant, .16-.35 mm long, .16-.33 mm broad, subquadrate or suborbicular, 1-3 times broader than the stem, base more or less auriculate, bifid for ⅓ their length; lobes subulate or triangular, acute or subobtuse; sinuses round or crescent-shaped; margin plane or reflexed, entire; median leaf cells 9-24 μ in upper part of dorsal lobe; walls thick; trigones and intermediate thickenings

none or very inconspicuous; dioicous; female inflorescence terminal on short branch; bracts 2-3 pairs, unequally bilobed; dorsal lobe ovate or lanceolate-ovate, acute, entire; lobules subulate or lanceolate or rarely foliate, tubulate or canaliculate, inner margin except for a laciniolate segment entire; bracteoles connate with base on 1 side, bifid to middle; lobes subulate or lanceolate, acuminate, margin entire except for basal laciniolate segment; perianth ovoid, 1.6-2 mm long, 1-1.2 mm broad, abruptly contracted to a short beak, ventrally 1-keeled, smooth; androecium subglobose; bracts 2-5 pairs; capsule and spores wanting.

On rocks, logs and living wood. Seattle (Piper), 1891; Roy (Allen), 1901; Seattle (Frye), 1904; Guemes Island (Frye), 1905; Gate (Foster), 1911; Dungeness (Foster), 1913.

Oregon: Powers (Foster), 1910; Alsea (Van Wert), about 1923; Santiam National Forest (Van Wert), about 1923.



Frullania californica. 1. Part of plant, dorsal view, $\times 2.5$. 2. Part of female plant, dorsal view, $\times 27.5$. 3. Part of female plant, ventral view, $\times 27.5$. 4. Dorsal leaf lobe showing scattered discolored cells, $\times 27.5$. 5. Median cells of dorsal lobe with few discolored cells, $\times 352$.

Order Anthocerotales

Gametophyte thalloid, flat, orbicular or semiorbicular or ribbon-like and subdichotomous, more or less lobed or dissected radially, without a well defined costa, of several layers of cells, compact or with interior mucilaginous cavities or rarely with intercellular air-

spaces; dorsal surface without differentiated epidermis; pores present on ventral and rarely on dorsal surface, cleft-like; cells with a single large chloroplast enclosing the nucleus; sex organs embedded in thallus; archegonial wall same as the surrounding tissue, reaching dorsal surface at maturity by means of a neck canal; antheridia arising endogenously, single or in groups, 2-4 occupying cell-cavities, separated from dorsal surface by 2-3 layers of cells, layers ruptured at maturity; calyptra none; involucre tubular, formed of archegonial wall and adjacent tissue, ruptured by elongating capsule; sporophyte consisting of an elongated pod-like capsule, a bulbous foot, and a short intermediate growing region; capsule dehiscing from apex downwards by 2 valves; valve-walls containing chlorophyll, having stomates with crescent-shaped guard cells; columella more or less persistent, filiform, surrounded thruout by spore-forming cells; spores more or less clearly tetrahedral, smooth or verruculose or echinulate or papillate, ripening from apex downward; elaters elongated, more or less contorted, often branched filaments of 2-4 cells; rarely cubical or with rudimentary thickenings present. Only the following family found in our territory.

Family **ANTHO CEROTACEAE**

Description the same as for the order. We have only the following genus.

ANTHOCEROS

Thallus suborbicular, variously lobed or dissected, sometimes ribbon-shaped and dichotomous, of more than 1 layer thruout; costa none or indistinct; monoicous; capsule long, erect, bivalved, exceeding the involucre; stomates always present; spores papillate or tuberculate or echinulate or rarely smooth; sterile cells without spiral thickenings.

A. Spores black.

B. Spores 36-46 μ ; elaters 50-110 μ long, of 1-2 or rarely 3 cells.

1. *A. punctatus*

BB. Spores 45-63 μ ; elaters 60-250 μ long, of 1-4 cells.

2. *A. fusiformis*

AA. Spores yellow.

C. Convex side of spores with numerous projections; elater geniculate.

D. Thallus with definite costa, its cross section with many air chambers.

3. *A. hallii*

DD. Thallus without definite costa, its cross section without air chambers.

4. *A. laevis*

CC. Convex side of spores with 8-15 crescentic warts; elaters contorted.

5. *A. pearsoni*

Comparison of species of <i>Anthoceros</i>	1. punctatus	2. fusi- formis	3. hallii	4. laevis	5. pearsoni
Spores black, yellow.....	b	b	y	y	y
Convex side of spores with many, or how many projections.....	m	m	m	m	8-15
Elaters geniculate, contorted.....	g	g	g	g	c
Thallus with definite costa.....	—	—	+	—	+
Cross section of thallus with large, small, or no air chambers.....	l	s		n	
Convex side of spore with spines, papillae, crescentic warts.....	s	p	p-w	p	w
Diameter of spores in μ	36-46	45-65	40-60	46-56	35-50
Number of cells thallus is thick in middle.....	8-12	10-25	6-8	6-8	6-11
Cross section of thallus with many air chambers.....	+	+	+	—	+
Number of cells elaters are long....	1-3	1-4	1	1-4	1-4
Plane surfaces of spores smooth, granulose, papillate.....	s-g	g-p	s-p	g-p	s

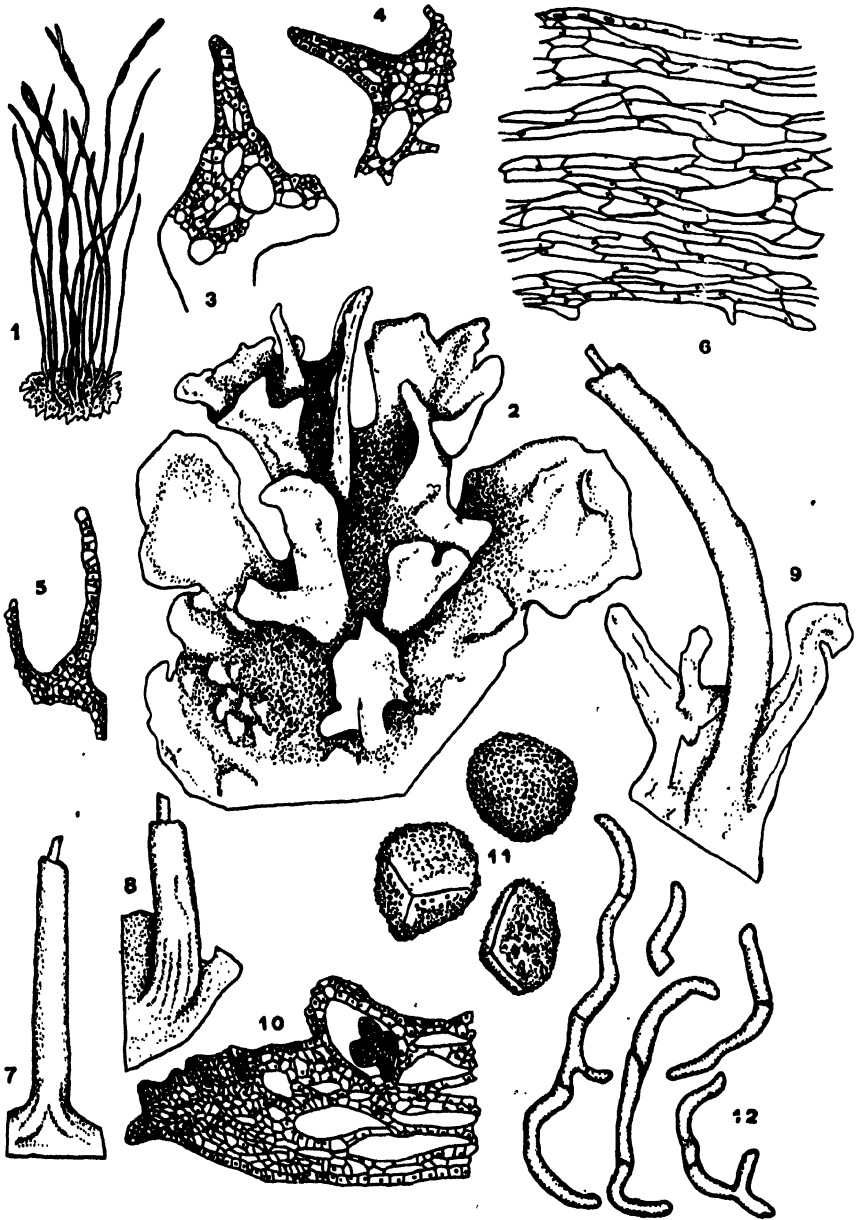
1. ***Anthoceros punctatus*** Linne, Sp. Pl. p. 1139. 1753.

Anthoceros scariosus Austin, Proc. Acad. Nat. Sci. Philadelphia 1869:230. 1869.

In pale green patches, black when dried, thallus 5-12 mm in diameter; margins ascending, undulate, lobed; lobes cuneate; dorsal surface more or less warty, more or less lamellate, without midrib; 8-12 cells thick in middle, 2-3 cells thick at margin; epidermal cells with 1 large chloroplast, the interior cells larger than epidermal, hyaline, air chambers large and numerous; involucre cylindrical, narrowed toward top, apex truncate, 20-30 μ long; stomates variable in length and width; spores 36-46 μ , black, convex face with numerous spines; elaters 50-110 μ , mostly 1-2 cells long, rarely 3, brown, geniculate; antheridia 2-5 in small receptacles, scattered on dorsal surface.

Moist soil, banks and sides of ditches. Aberdeen (Foster), 1909; Montesano (Grant), 1917.

Oregon: Portland (Foster), 1905.



Anthoceros fusiformis. 1. Plant, $\times 1$. 2. Portion of thallus, $\times 23$. 3. Vertical section of anterior margin of thallus segment, $\times 53$. 4 and 5. Vertical section of dorsal lamellae, $\times 53$. 6. Nearly median longitudinal section of thallus segment, $\times 53$. 7-9. Involucres, $\times 12$. 10. Vertical longitudinal section near thallus apex, showing antheridia and archegonia, $\times 53$. 11. Spores, $\times 305$. 12. Elaters, $\times 305$. (After Howe).

2. **Anthoceros fusiformis** Austin, Bull. Torrey Bot. Club 6:28. 1875.

Plants bright to dark green, somewhat orbicular, radiately dissected, rosette-shaped, 5-15 mm in diameter, sometimes ascending and caespitose, opaque, rigid, 10-25 layers of cells thick in center, abruptly thinned to 2-3 cells at margin, without a definite costa; surface cells 30-75 μ long, 18-40 μ wide, each containing a single large chloroplast; inner cells loose with air-cavities between them; margin often with large glandular thickenings, more or less lamellate-crisped; lamellae often leaf-like; monoicous; involucre bracts numerous, crowded, 2 mm long, .3-5 mm broad, narrowly cylindric or more or less fusiform, bases not united in pairs, smooth or grooved, mouth repand or dry and torn; capsule dark brown or black, 2-8 cm long, 2-5 mm wide; stomates rather abundant, guard cells colorless; spores black or very dark brown, angular 45-63 μ , convex side papillose; papillae very abundant, never over 3 μ long; straight surface granulose-papillate, 40-63 μ in widest part; elaters geniculate, more or less contorted, 1-4-celled, sometimes branched, .06-.25 mm long.

On moist banks. Seattle (Frye), 1904; Queets and Elwha River valleys in Olympic Mountains (Frye), 1907; Nahcotta (Frye), 1908; Ilwaco (Frye), 1908; Mount Rainier (Foster), 1909, 1911; Montesano (Foster), 1909; Brinnon (Foster), 1911; Seattle (Rigg), 1911; Potlatch (Foster), 1912; Lake Cushman (Foster), 1912; Heybrook (Clark), 1913; Olympic Hot Springs (Foster), 1914; Port Angeles (Foster), 1914; Friday Harbor (Clark), 1923; Seattle (Roberts), 1923; Cascade Mountains (Grant), 1925; Lakota (Clark), 1928.

Oregon: Mt. Hood (31); Portland (31); Oakland (Hunt), 1912; Alsea (Van Wert), about 1923.

Idaho: Moscow Mountain (Clark), 1923.

2a. Var. **stomatifer** (Austin) Howe, Bull. Torrey Bot. Club 25:18. 1898.

Anthoceros stomatifer Austin, Bull. Torrey Bot. Club 6:28. 1875.

Capsule slender, 4-9 cm long and .25-.4 mm thick, valves much twisted in drying; spines of the spores sometimes exceeding 3 μ in length; elaters rather broader than in the type.

Howe (37) says "*A. fusiformis stomatifer* is in some respects intermediate between *A. fusiformis* and *A. punctatus*. It seems to have nothing in thallus, involucre, or number of stomates on the cap-

sule wall to distinguish it from *A. fusiformis* and is scarcely distinguishable from *A. punctatus* except by the longer narrower involucre, the longer capsule, more twisted valves and rather larger spores with much more abundant spines. It intergrades perfectly with the genuine *A. fusiformis*."

We have not seen authentic material. From the description we doubt whether it is worthy of varietal rank.

Tacoma (45).

Oregon (3).

3. ***Anthoceros hallii*** Austin, Bull. Torrey Bot. Club 6:26. 1875.

Anthoceros sulcatus Austin, Bull. Torrey Bot. Club 6:27. 1875.

Thallus smooth, thin, prostrate, rarely ascending, irregularly dissected; larger segments linear or fan-shaped, 5-20 mm long, 2-4 mm wide, sometimes dichotomously branched or lobed; sterile and fertile stems nearly the same thickness thruout; costa present; margin crisped; lobes with large flat brown thickenings; monoicous; involucre numerous, bases not united, yellowish green to light brown; mouth repand or entire or lacerate; capsule yellowish brown, elongated-cylindric; valves thin; stomates abundant; spores yellow or yellow-green, angular, convex surface papillate or with large numerous warts, straight surface smooth or slightly papillate; elaters small, not very abundant, 1-celled, geniculate, contorted, colorless or a dilute brown.

. On ground in wet meadows, with mosses. Seattle (Piper), 1892.

Oregon: Salem (8).

4. ***Anthoceros laevis*** Linne, Sp. Pl. p. 1139. 1753.

Anthoceros oregonus Austin, Bull. Torrey Bot. Club 6:26. 1875.

Anthoceros mohrii Austin, Bull. Torrey Bot. Club 6:304. 1879.

Thallus dark green,, 5-15 mm in diameter, nearly flat, smooth, divided into broad obovate lobes, not costate, rounded at apex, margins entire or crenate; transverse sections 6-8 cells high in the middle, without lacunae, surface cells 35-70 by 30-35 μ ; monoicous; involucre sometimes geminate, 2-3.5 mm long, .7-1 mm wide, cylindrical, slightly narrowed toward the apex, the mouth repand; antheridia in groups of 2-3, in receptacles scattered on the dorsal surface of the thallus; capsule 15-25 mm long, 3.5-5 mm wide, brown; stomates 70-77 by 25-30 μ ; spores 46-56 μ , greenish yellow, thickly granulate-papillate; elaters pale brown, of 1-4 cells; the cells 25-45 μ , geniculate. (Adapted from MacVicar).

Oregon: Salem (3).

We have not seen the specimen and include the species on the basis of the report above.

5. **Anthoceros pearsoni** Howe, Bull. Torrey Bot. Club 25:8. 1898.

Plants smooth, prostrate or ascending, irregularly lobed; segments linear or fan-shaped, 5-10 mm long, 1-5 mm wide, dichotomously branched or again lobed, without apical ventral costa, 6-11 layers thick in the center, 3-4 layers at margins; fertile stem with lamina of 2-3 cell-layers; margin thin, crisped; lobes round, green, sometimes stalked, never bearing rhizoids; surface cells rhombic, inner cells a little larger but compacted; Nostoc colonies present; monoicous; involucre single or in pairs, more or less terminal, cylindric to elongated-cylindric, light green or yellowish brown, sometimes decumbent; mouth entire or repand-dentate, or lacerated with age; capsule light brown or yellow, sometimes grooved, 10-35 mm long; valves thin; stomates present; columella filiform, naked; spores yellow or greenish, convex side with 8-15 crescentic warts but otherwise smooth; elaters yellow or light brown, 1-4 cells long, contorted, often branched.

On moist ground. Seattle (Piper), 1892.

Oregon: Seaside (Foster), 1905.



Anthoceros pearsoni. 1. Segment of thallus with mature sporophyte, $\times 1$. 2. Portion of sterile thallus, (t) beginning of marginal glandular thickening, $\times 1$. 3. Small part of thallus showing marginal glandular thickenings (t) fully developed, $\times 6$. 4. Elaters, $\times 112$. 5, 6. Spores, $\times 305$. (After Howe).

Glossary

A-, as a Greek prefix, not or without.

ACROGYNOUS, the archegonium arising from the apical cell.

ACUMINATE, gradually tapering to a point of 10° or less.

ACUTE, ending in a point less than a right angle and usually more than 10° .

ADHERENT, attached.

ADNATE, different whorls or unlike parts grown together.

ADVENTITIOUS, said of shoots which do not arise in the usual places.

ALAE, wings, expanded parts.

ALTERNATE, leaves or branches arising so there is only one at any given height of stem.

ALVEOLATE, resembling a honey comb.

AMENT, an elongated axis covered with imbricate bracts which protect reproductive organs.

AN-, same as a-.

ANACROGENOUS, the archegonium arising from cells left behind by the apical cell.

ANDROECIUM, the antheridia together with the bracts and parts of the stem associated with them.

ANNULAR, ring-like.

ANTERIOR, the front; the part nearest the growing point.

ANTHERIDIUM, the body which forms the sperms.

ANTICAL, dorsal.

APICAL, pertaining to the apex.

APICULATE, tipped with a small point, or apiculus.

APPENDICULATE, with an appendix or an extension.

APPRESSED, closely pressed to the stem.

APPROXIMATE, close together, as distinguished from distant and imbricate.

ARCHEGONIUM, the flask-like female reproductive organ.

ARCULATE, bent in a curve like a bow.

AREOLAE, the small spaces into which a surface may be divided.

AREOLATE, having surface apparently marked off into areas (areolae),

ASCENDING, rising from a more or less prostrate base.

ASSIMILATIVE TISSUE, the part of the thallus where the green cells are found.

ATTENUATED, becoming thinner or being drawn out.

AURICULATE, furnished with small lobes at the basal angle of the leaf.

AUTOICOUS, having both male and female reproductive organs on same branch.

AXIL, the forward angle between the leaf and the stem.

AXILLARY, pertaining to or growing in the axil.

AXIS, central line of thallus or stem.

BEAKED, ending in a prolonged narrow tip (said of perianth),

BI-, twice.

BIDENTATE, having two teeth.

BIFID, cleft into two divisions to about the base.

BILABiate, 2-lipped.

BILOBED, having two projections or division, said of leaves.

BIPINNATE, pinnate and then each part again pinnate.

BISTRATOSE, composed of two layers or strata of cells.

BORDERED, having the cells of the margin different from the others.

BRACTEOLES, modified underleaves near the reproductive organs.

BRACTS, modified leaves near the reproductive organs.

CADUCOUS, falling off early.

CAMPANULATE, bellshaped.

CAESPITOSE, growing in turf-like patches or tufts.

CALYPTRA, the thin hood or veil which covers the capsule.

CANALICULATE, channeled, or with deep longitudinal grooves.

CAPSULE, the closed case containing the spores.

CAPILLARY, resembling a hair in form.

CAPITATE, head-like.

CARINA, a keel.

CARINATE, keeled.

CAULESCENT, having an obvious stem.

CAULINE, of or belonging to the stem.

CHLOROPHYLL, the green substance in the protoplasm of plants.

CILIATE, having cilia or hair-like processes, commonly marginal and forming a fringe like the eyelashes.

CILIOLATE, diminutive of ciliate.

CLAVATE, slender below and thickened above, club-shaped.

CLEFT, cut into lobes somewhat past the middle.

CLUSTERED, collected into a bunch.

COALESCENT, grown together.

COHERENT, united or grown together from their beginning.

COLUMELLA, a column-like structure in the capsule of the Anthocerotales.

COMPLANATE, flattened, or nearly in the same plane.

COMPLICATE, folded together.

COMPLICATE-BILOBED, 2-lobed with one lobe folded under and against the other.

COMPRESSED, flattened.

CONCOLOR, of one color.

CONCAVE, with edges turned so as to make a pocket or cave on the stem side.

CONDUPPLICATE, folded lengthwise on itself along the midrib, so that the two halves are face to face.

CONFLUENT, blended into one, growing together so as to obliterate all distinction of separate parts.

CONNATE, united or grown together from the first formation.

CONNIVENT, converging or brought close together.

CONTIGUOUS, in actual contact but not overlapping.

CONTORTED, twisted.

CONTRACTED, either narrowed or shortened.

CONIC, CONICAL, circular at the base and tapering to a point, cone shaped.

CONVOLUTE, rolled up lengthwise.

CORDATE, heartshaped, with attachment at broader part.

CORIACEOUS, resembling leather in texture.

CORTICAL, of the cortex, or outside.

COSTA, the rib or vein of a leaf or thallus, usually composed of slightly differentiated cells.

CREeping, growing flat on the ground.

CRENATE, the edge scalloped into rounded teeth.

CRENULATE, minutely or slightly crenate.

CRISPATE, curled and contorted; crisped.

CRUCIATE, like a cross.

CRYSTALLINE, shining.

CUCULATE, hoodshaped.

CUNEIFORM, wedgeshaped.

CUTICLE, a layer of tough substance covering the surface of a leaf, stem or other structure.

DECIDUOUS, falling off, or subject to falling, not persistent.

DECOLORATE, deprived of color.

DECUMBENT, prostrate but with ascending tip.

DECURRENT, said of leaves prolonged on the stem below their insertion.

DECURVED, turned back.

DEFLEXED, bent downwards.

DEHISCENCE, the regular splitting open of the capsule.

DENTATE, toothed, the teeth pointing outward, not downward.

DENTICULATE, with small teeth.

DI-, two, double.

DICHOTOMOUS, divided into two branches which are equal or nearly so, often repeatedly so.

DIMORPHOUS, of 2 forms.

DIOECIOUS, dioicous.

DIOICOUS, with archegonia and antheridia on separate plants.

DISCSHAPED, diskshaped.

DISKSHAPED, flat and round.

DISSECTED, cut deeply into many lobes or segments; depth indefinite.

DISTANT, said of leaves separated about their own length or more.

DISTICHOUS, having the leaves inserted in two rows.

DIVERGENT, spreading out or away from each other.

DIVIDED, cut into segments to base or nearly so.

DOLIFORM, barrelshaped or like a cask in form.

DORSAL, pertaining to the upper side of the leaf or thallus.

DORSI-VENTRAL, pertaining to the upper and lower surface.

E-, means destitute of; e. g., ecostate, without costa or midrib.

ECHINATE, armed with prickles.

ECHINULATE, having small prickles.

EFFUSE, very loosely branched and spreading.

ELATERS, sterile cells with spiral bands, which are mixed with the spores.

ELLIPSOIDAL, approaching the elliptic in form.

ELLIPTIC, elliptical.

ELLIPTICAL, oval or oblong with both ends of the same width.

EMARGINATE, having a small notch at the tip.

EMBEDDED, sunken in surrounding tissue.

EMERGENT, partly projecting, as the capsule out of the perianth.

EMERSED, about half projecting, as the capsule out of the bracts.

ENDOGENOUS, growth by additions from inside, as of the stem.

ENTIRE, margin without notches or projections other than a single notch or projection at the tip.

EPIDERMIS, the outer one or more layers of cells, as of a leaf.

ERECT-PATENT, spreading at an angle of 45° or less.

EROSE, margin as if gnawed.

EROSE-DENTATE, with quite irregularly placed teeth; as if gnawed into teeth.

EVOLUTE, rolled out.

EXOGENOUS, growth by the addition of outside layers, as of the stem.

EXPLANATE, spread out or flattened out.

EXSERTED, elevated above the surrounding parts.

FALCATE, curved like a sickle.

FASCICULATE, in dense tufts.

FASTIGIATE, branches roughly parallel and reaching about the same elevation.

FILAMENT, a slender thread-like body.

FILIFORM, long, slender, cylindric; thread-shaped.

FIMBRIATE, fringed, furnished with fringe.

FLAGELLA, flexible slender string-like branches.

FLAGELLIFORM, slender, like a flagellum.

FOLIACEOUS, having the texture and nature of a leaf.

FOOT, basal portion of the sporophyte.

FREE, not united with any other organ.

FROND, the organ formed by the union of the stem and leaves; or a portion neither distinctly stem nor leaf.

FRONDOSE, resembling a frond.

FURCATE, forked.

FUSCOUS, dull brown.

FUGACEOUS, lasting but a short time.

GAMETOPHYTE, that generation of the plant which bears the sexual organs.

GALEATE, shaped like a helmet.

GEMMAE, bud-like bodies capable of reproducing the plant.

GEMMIFEROUS, bearing gemmae.

GEMMIPAROUS, gemmiferous.

GENERA, plural for genus, the first of the two terms of a double scientific name.

GENICULATE, bent abruptly at an angle.

GLABROUS, smooth in the sense of having no hairs or bristles or other pubescence.

GLAUDESCENT, dull-green passing into a greyish blue; being covered with a fine white powder easily rubbed off.

GLAUCOUS, bluish gray.

GLOBOSE, spherical or nearly so in form.

GRANULAR, composed of grains; as if powdered with grains.

HABITAT, the situation in which a plant grows in the wild state.

HAIRY, beset with hairs, specially long ones.

HETEROICOUS, the plant both paroicous and monocous.

HEXA-, six.

HEXAGONAL, six-sided.

HIRSUTE, clothed with stiff or beard-like hairs.

HISPID, beset with stiff hairs.

HORIZONTAL, in a straight line with the stem.

HYALINE, transparent or nearly so, colorless.

IMBRICATE, overlapping one another like the tiles or shingles on the roof.

IMMERSED, the perianth is immersed when the bracts enclose it.

INCISED, cut deeply and irregularly.

INCISED-CILIATE, cut deeply and sharply into cilia.

INCLUDED, enclosed, when the part in question does not project beyond another.

INCUBOUS, the upper margin overlapping the lower margin of the leaf next in front as viewed from the upper side of the plant.

INCURVED, gradually curving inward toward the stem.

INFERIOR, situated below some other organ; farthest from the growing point.

INFLATED, hollow and distended.

INFLEXED, incurved.

INFLORESCENCE, that part of the stem which bears either archegonia or antheridia.

INNOVATION, a new shoot, usually from just below the perianth.

INVERTED, turned upside down.

INVOLUCRE, the circle of single or united bracts surrounding the perianth.

INVOLUTE, margin rolled inward.

ISODIAMETRIC, having the diameters equal or nearly so, referring to cells when not elongated.

JULACENT, resembling a catkin.

JULACEOUS, narrow, cylindrical and smooth.

KEEL, the projecting ridge on the folds of some leaves.

KEELED, furnished with a keel.

LABIATE, lipped.

LACERATE, irregularly cleft as if torn.

LACINIAE, the lobes of a lacinate organ.

LACINIATE, cut irregularly into narrow lobes; applied to the margin of leaves and bracts and perianth.

LACUNOSE, having pits or depressions.

LAMELLA, a plate of tissue, a high narrow ridge.

LAMINA, the blade or expanded part of the thallus as distinct from the costa.

LANCEOLATE, shaped like a lance.

LATERAL, proceeding from, or fixed on or near, the side of the stem or other organ.

LEATHERY, of the consistency of leather, coriaceous.

LINEAR, many times longer than broad, with parallel margins.

LOBATE, lobed, possessing lobes.

LOBE, a rounded projection or division of a leaf or other flattened organ.

LOBULE, a small lobe.

LOCULUS, plural loculi; cell or compartment.

LUMEN, the cell-hollow.

MAMILLATE, having convex protuberances ending in a short point.

MARGINAL, belonging to the margin.

MARGINATE, having the edge different from the rest, as of leaf or thallus.

MEDIAL, median.

MEDIAN, belonging to the middle of the leaf or thallus.

MICRON, plural micra, the thousandth part of a millimeter.

MIDRID, the differentiated central portion of a leaf or thallus.

MONOEICIOUS, monocious.

MONOICIOUS, having antheridia and archegonia on the same plant.

MU, the Greek letter μ , the abbreviation for micron.

MUCRONATE, abruptly pointed with a short sharp spine.

NAKED, surface without covering or hairs.

NERVE, costa, vein, rib.

NODOSE, jointed or swollen.

OB-, as a prefix usually signifying inversion; upside down.

OBCONIC, conical but with the point of attachment at the apex of the cone.

OBCONICAL, obconic.

OBCORDATE, heartshaped with narrower part at the base.

OBLONG, elliptic and 2 or 3 times as long as wide.

OBOVATE, inversely egg-shaped; attached by small end.

OBOVOID, inversely ovoid.

OBTUSE, blunt or rounded at the end.

OLEAGENOUS, with an oily or fatty lustre

OLIVACEOUS, dull dark green, olive green.

OPERCULATE, having a lid, said of the capsule.

ORBICULAR, circular or nearly so and flat.

OVAL, forming a broad ellipse.

OVATE, applied to a leaf or other flattened organ whose outline resembles that of an egg.

OVATE-LANCEOLATE, between ovate and lanceolate.

OVATE-OBLONG, between ovate and oblong.

OVoid, ovate or oval in a solid form.

PALLESCEnt, very light green.

PALMATE, lobes or branches spreading from a common center like the fingers of the hand.

PAPILLAE, small glandular excrescences resembling nipples.

PAPILLATE, producing papillae.

PAPILLOSE, same as papillate.

PARAPHYLLIA, minute leaf-like or much-branched organs among the leaves.

PARAPHYSES, jointed filaments mixed with the antheridia.

PARENCHYMA, consisting of cellular tissue only; cells commonly thin-walled, not elongated.

PAROICous, monoicous with the 2 kinds of sex organs on the same branch.

PARTED, applied to leaves when they are divided to the middle or below.

PATENT, spreading wide apart.

PEDICEL, stalk, as of the capsule.

PELLUCID, clear or transparent.

PENTA-, five.

PENTAGONAL, 5-angled.

PERIANTH, a special open tubular organ formed by the coalescence of modified leaves and surrounding the archegonia.

PERICHAETIAL, applied to the bracts about the antheridia or base of sporophyte.

PERIGONIUM, leafy envelope surrounding the antheridia.

PERIGYNIUM, leafy envelope surrounding the archegonia, used sometimes in place of perianth.

PERSISTENT, not falling off, lasting.

PINNATE, laterally arranged equidistant branches, spreading on each side like a feather.

PLICATE, folded in pleats or furrows lengthwise, like a fan.

PLUMOSE, feathery, resembling a feather.

POLYOICous, two kinds of sex organs on different plants.

PORES, small often roundish holes or apertures in the epidermis of the gametophyte.

POSTICAL, ventral, referring to the under side of a plant.

- PROCESSES, any projections from the surface or edge of a body.
- PROCUMBENT, flat on the ground or surface.
- PROSENCHYMATOUS, woody.
- PSUEDO-, false, not true.
- PSUEDO-PERIANTH, perianth-like in appearance, but yet not a perianth.
- PUBESCENT, downy, covered with soft hairs.
- PUNCTATE, dotted with minute holes or with what looks like holes.
- PYRIFORM, pear-shaped.
- QUADRATE, 4-sided.
- QUADRATE-ORBICULAR, between quadrate and orbicular.
- QUADRI-, four.
- RADIAL, arranged in rays.
- RADICULOSE, producing a number of rhizoids, or radicles.
- RAMOSE, branching.
- RECEPTACLE, shortened stem or branch on which floral organs are inserted.
- RECURVED, curved outwardly or backwardly from the stem.
- REFLEXED, bent outwardly or toward the dorsal side.
- REGULAR, of the same shape and number.
- RENIFORM, kidney-shaped.
- REPAND, margin of leaf, when like a wavy line.
- RETICULATE, forming a network, applied to the veins.
- RETUSE, terminating in a round end which is indented.
- RHIZOID FURROW, a groove in the stalk of the receptacle of Marchantiaceae.
- RHIZOIDS, organs resembling roots but simpler in form, and in the liverworts always single thread-like cells.
- ROSETTE, a whorl of leaves or other organs from a point on the ground.
- ROTUND, having a circular outline.
- RUGOSE, applied to a surface when rough or wrinkled.
- SAC, any closed membrane or deep purse-like body.
- SACCATE, having the form of a sac or bag.
- SCABROUS, rough or harsh to the touch.
- SCALE, a minute rudimentary leaf.
- SECUND, with all leaves or organs turned toward one side.
- SEGMENTS, a subdivision or a lobe of any cleft body.
- SEMI-, half.
- SEMIANNULAR, forming a half ring.
- SEPTATE, divided by walls.
- SERRATE, toothed, the teeth sharp and pointing forward like the teeth on a saw.
- SERRULATE, diminutive of serrate.
- SESSILE, without a stalk.
- SETA, the stalk of the capsule.
- SHEATH, a thin membranous body which is wrapped around the stem or other organ.
- SHEATHING, encircling the stem or other organ.
- SIMPLE, without subdivisions or branches.
- SINUATE, margin alternately bent inward and outward.
- SINUS, the reentering angle between lobes and projections.
- SMOOTH, without roughenings, not pubescent.
- SOLITARY, single, not associated with others.

SPARINGLY, not abundantly, not plentifully.

SPHERICAL, resembling a sphere.

SPINOSE, having sharp and rigid teeth.

SPINULOSE, diminutive of spinose.

SPIRAL, twisted like a screw.

SPORE, name applied to the asexual reproducing cells.

SPOROONIUM, a simple sporophyte.

SPOROPHYTE, the spore-bearing generation, consisting of the capsule and the seta.

SPUR, any projecting appendage on the leaf.

SQUAMATE, furnished with scales.

SQUARROSE, at right angles to the stem.

STALK, stem or petiole.

STELLATE, shaped like a star.

STERILE, unproductive.

STOLONS, slender stems with minute leaves.

STOMATES, openings thru the epidermis of the sporophyte, bordered by 2 special cells.

STRIATE, roughened with fine longitudinal lines.

STYLUS, a small awl-like lobe.

SUB-, somewhat, nearly.

SUBULATE, tapering from broad base to a sharp point.

SUCCUBOUS, the anterior margin covered by the posterior margin of the next leaf in front as seen from the upper side of the plant.

SUPERIOR, nearest to the growing point.

TERETE, circular in cross section.

TERMINAL, placed at the end of a stem or branch.

TETRA-, 4.

TETRAD, a group of 4 spores not yet fallen apart.

TETRAHEDRAL, 4-sided and solid.

THALLUS, a plant body not differentiated into stem and leaf.

TOOTHED, furnished with sharp projections, especially like saw teeth, but not pointing forward.

TRANSVERSELY, said of leaves when attached across the stem.

TRI-, 3.

TRICHOME, a general term for a plant hair or any of its modifications.

TRIDENTATE, 3-toothed.

TRIFID, lobed or cleft into 3 segments.

TRIGONES, thickenings of the walls where 3 cells meet.

TRIGONOUS, having 3 obtuse angles.

TRIQUETRUS, having 3 acute angles.

TRUNCATE, ending abruptly as if cut off.

TUBERCULATE, beset with small wart-like projections.

TYPE, the specimen from which the original description was made; the usual form.

UNDERLEAVES, a third row of leaves on the ventral side of the stem in some of the Jungermanniaceae.

UNDULATE, wavy or with wavy margin.

UNI-, 1.

UNILABATE, 1-lipped.

UNISTRATOSE, of 1 layer of cells.

UNSYMMETRICAL, UNSYMMETRIC, parts of a different shape or size.

URCEOLATE, urnshaped.

VAGINATE, sheathing.

VALVE, one of the parts of the dehiscing capsule.

VENTRAL, pertaining to that side of the plant which is next to the ground.

VENTRICOSE, inflated or swelled out at one side.

VERRUCOSE, warty, beset with little projections.

VERRUCULOSE, diminutive of verrucose.

WAVY, the surface or margin alternately concave and convex, sinuous.

WING, any membranous expansion.

WINGED, having a wing.

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Megalocotyle Marginata, a New Genus of Ectoparasitic Trematodes From the Rock Fish

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INTRODUCTION

An examination of 27 Yellow-Spotted Rock-Fish, *Sebastes nebulosis* (Ayres), from the San Juan Archipelago, during the summers of 1927 and 1928 at the Puget Sound Biological Station, showed that all except one harbored on the gills 1-22 ectoparasitic trematodes. These are put in a new genus of the family Tristomidae. This genus and its single species are herein described and an account given of the morphology.

To Dr. J. E. Guberlet of the University of Washington the writer wishes to express her gratitude for many helpful suggestions and for his assistance in the preparation of this paper.

The trematode is present most commonly on the gill arches, and since it is of a translucent, yellowish-white color, lying flattened between the gill rakers, it is barely discernable unless it is in motion. The worm attaches itself by means of the posterior sucker (fig. 3, ps), securing itself to the tissues by means of the hooks, and frequently producing minute lesions on the gill arch at the point of attachment. In moving, it alternately attaches and detaches the anterior and posterior suckers in a leech-like manner. Its food consists of the mucus matter present on the gills and in the gill chamber.

The worms were most successfully studied in the living condition. Specimens were anaesthetized with chlorotone, killed under pressure of thin glass, and preserved in 70% alcohol. For whole mounts they were stained either in Ehrlich's or Delafield's haematoxylin and destained in 8% acid alcohol. Sections were stained in Delafield's haematoxylin and counterstained with eosin.

RELATIONSHIPS

The trematode herein described as a new genus conforms to the characteristics of the family Tristomidae (Tasch.:Pratt; 1900) as given by Pratt (1916:173). Trematodes of this family possess a

single large, round terminal sucker, often armed with hooks; a pair of smaller anterior suckers; ventral mouth just behind the anterior suckers; paired eye spots; anterior genital pores, either common or separate. They are usually on marine fishes.

The following generic description based upon one type species may include some characters which are merely specific.

MEGALOCOTYLE, new genus

Body flat, thin, elongate; anterior suckers 2, circular or elliptical, one on either side and in front of the mouth. Fixation disc one, at posterior end of body, circular, with marginal membrane; internal surface divided into a central and a number of peripheral areas by means of radial septa some of which may bifurcate; hooks 3 pairs, near posterior border of disc. Mouth subterminal. Testes 2. Common genital pore on left margin of body behind anterior sucker; vaginal opening just posterior to it. Eye spots two pairs. Type species the following:

Megalocotyle marginata, new species

Body flat, elongated, 1.92-4.43 mm long; breadth one-third the length. Anterior suckers elliptical, attached at apices of shallow indentations. Posterior disc as wide as body, with marginal membrane thrown into folds; internal surface divided into a central pentagon and 7 peripheral areas by 5 radiating septa, of which the posterior two bifurcate; hindmost area continuous with central; hooks 3 pairs, in the two posterior septa; length of all hooks approximately equal; foremost pair broad; disc with 14 minute chitinous rods along margin. Mouth behind anterior suckers; pharynx large; oesophagus short; intestinal crura with numerous short branches laterally and only a few medially. Common genital opening on left margin of body just behind anterior sucker, leading into genital atrium. Testes paired, large, ovate, in center of body between intestinal trunks; vas deferens proceeding forward with numerous complicated convolutions finally opening into genital atrium; prostate gland at right of other genital organs, large, egg-shaped, with thick wall, and communicating with the penis by means of heavy-walled duct. A pair of small oval bodies behind testes. Ovary in median line, in front of testes; oviduct arising on dorsal side of ovary, proceeding forward with slight turnings to group of mesenchymous cells which it enters dorsally, emerging on the ventral side, and opening into heavy walled pyriform ootype; ootype opening into genital atrium by means of short uterus;

vitellaria extending posteriorly from anterior sucker on right and genital ducts on left, occupying all space lateral to and posterior to genital organs; paired yolk ducts forming vitelline reservoir in front of and to right of ovary; short unpaired yolk duct arising dorsally to join oviduct; vaginal opening on left lateral margin just posterior to common genital opening; vaginal canal enlarged into pear-shaped seminal receptacle at level of ootype, and opening into anterior of yolk reservoir; eggs stalked, tetrahedral.

Habitat. Gills of *Sebastes nebulosus* (Ayres).

Locality. Friday Harbor, Washington.

FORM OF BODY

The body is much flattened and in outline it is elongated, measuring 1.92-4.43 mm x 0.58-1.23 mm. The breadth is approximately one-third the length and practically uniform thruout. In cross section the body is flat on the ventral side and slightly convex on the dorsal. The posterior end is rounded and is continued into the large fixation disc as in *Epibdella*. The anterior border is slightly concave, and separated from the lateral borders by a shallow notch on each side, in which are attached the anterior suckers (fig. 3). Below are given measurements of three worms of different lengths (all measurements in millimeters):

Length of body, including posterior sucker.....	1.92	1.85	4.43
Breadth of body at anterior end of testes.....	0.58	0.91	1.23
Length of anterior sucker.....	0.25	0.45
Breadth of anterior sucker.....	0.18	0.26
Diameter of posterior sucker with membrane.....	0.58	0.85	1.24
Length of anterior hook.....	0.07	0.12	0.15
Length of middle hook.....	0.09	0.14	0.10
Length of posterior hook.....	0.13	0.14	0.11
Length of chitinous rod in sucker.....	0.018
Egg at broadest edge.....	0.16

ORGANS OF ATTACHMENT

In general, the suckers resemble those of the genus *Tristomum* more closely than those of any other monogenetic trematode. The prominent anterior suckers (fig. 3, as) are paired at the anterior extremity of the body, in front of the mouth. They are slightly elliptical, attached to the body at the apices of shallow indentations that divide the anterior from the lateral margins of the body, and are directly continuous with the mesenchyme of the body.

The fixation disc (figs. 3, 9, ps) attached to the posterior end of the body is highly developed into a powerful adhesive organ. This

large flat, circular sucker has a diameter equal to the breadth of the body proper and one-third its length, and possesses a marginal membrane (fig. 9, mm) thrown into wavy folds. Five radiating septa (fig. 9, s) divide the ventral surface into marginal areas and a central gella subequa. Antennae with flagella nearly as long as the body, pentagon with the posterior septum lacking. The two radiating posterior septa are bifurcate at right angles, thereby forming two right-angled triangles with the margin. Thus there are 7 peripheral areas on the sucker, the hindmost of which is continuous with the central area.

Three pairs of hooks (figs. 3, 9, 10) are imbedded, one behind the other, in the two posterior septa. These protrude upon its ventral surface. The pair nearest the center of the disc is broad, with a few spines in the center. An enveloping sheath (fig. 10) imbeds the base of each of these two large hooks. The two slender posterior pairs are alike, twisted and each strongly recurved at the end nearest the border of the sucker. All three pairs are of approximately the same length, measuring 0.12, 0.14, 0.14 mm respectively, in a medium sized worm.

At intervals along the margin are 14 minute chitinous rods about 0.018 mm long (fig. 9, c). One is found in each of the 4 anterior polygons, one at the base of each upper branch of the bifurcate septum, 3 in each triangular area and two in the posterior area, as shown in figure 9. At the point of each chitinous rod the margin of the disc is slightly indented. Their location is uniform in all specimens of this species.

DIGESTIVE SYSTEM

The mouth (figs. 3, 6, m) is situated on the ventral side of the body at some distance behind the anterior suckers. It leads directly into a large, heavy-walled pharynx (figs. 3, 6, ph). This organ is composed largely of connective tissue, provided with both circular and longitudinal muscle fibers and a number of pharyngeal glands. The oesophagus (fig. 6, oe) is extremely short, receiving the openings of a number of unicellular salivary glands (figs. 6, 7, sa) arranged on either side of it, and leading into its cavity by short ducts. It leads directly into the two intestinal crura (fig. 7, i) which give off numerous branched diverticula both laterally and medially. The median branches are located primarily in that portion of the body posterior to the genital system.

EXCRETORY SYSTEM

The excretory system is very similar to that of *Epibdella*. Paired lateral vessels could be seen in cross section altho they were not found in whole mounts. Hence they are not shown in the figures. A large terminal reservoir (figs. 3, 7, er) is located on each side of the intestinal crura, in the anterior third of the body, and about one-fourth of the distance from the lateral margin. These open to the exterior by small dorsal pores (fig. 3, ep) situated on the level of the posterior margin of the pharynx. The vesicle walls are thin structureless membranes which are capable of considerable extension, depending upon the amount of the contained fluid.

NERVOUS SYSTEM

The brain (figs. 1, 3, 6, b) is situated just in front of the pharynx, in the dorsal side of the body. It is crescentic, arching around the pharynx, and giving off a number of branches. Anteriorly a number of branches are given off and again united by a semicircular commissure from which several short branches arise to supply the cephalic region, as figured. Posteriorly two main ventral nerves (fig. 3) are given off on each side, a small external and a larger internal trunk. Paired dorsal nerves have been mentioned by some writers in *Tristomum*, according to Goto (1895:76) and by Heath (1902:129) in *Epibdella squamula*, but no dorsal branches were satisfactorily demonstrated in *Megalocotyle marginata*.

REPRODUCTIVE SYSTEM

Both male and female organs of reproduction occur in the same individual, as in all monogenetic trematodes, occupying the space in the anterior half of the body between the two intestinal crura. A genital atrium similar to that of *Epibdella* as described by Goto (1895:234 and 1898:269) receives the penis and uterus, and opens on the left margin of the body just behind the anterior sucker. The genital system resembles that of *Epibdella sciamae* (P. J. van Beneden, according to Goto, 1898:269) more closely than that of any other trematode.

Male: Two ovate testes (figs. 2, 3, t) containing sperm in various stages of development are situated midway in the body, occupying all the space between the dorsal and ventral walls. Each is surrounded by a sheath of connective tissue. The vasa efferentia have not been observed, but no doubt they originate at the anterior edge

of each testis, as in *Epibdella*, and unite immediately to form the vas deferens (figs. 2, 8, vd) which is readily seen either in a whole mount, or in a living worm, as it is always filled with sperm. The vas deferens runs forward on the left of the ovary and yolk reservoir, then to the right on the dorsal side of the reservoir. Here it bends back upon itself to the left and then turns cephalad parallel to the vagina until it reaches the level of the anterior margin of the seminal receptacle and ootype. There the vas deferens turns again to the right and follows the prostate gland on its inner side. Finally it makes a large downward loop dorsal to the prostate gland in front of which it enters the penis. The prostate gland (figs. 2, 8, pr) is a large oval body to the right of the other genital organs, filled with an evenly staining, homogeneous mass. A heavy walled canal (fig. 2, pd) containing material from the gland communicates with the penis.

Just behind the testes is a pair of small oval bodies (figs. 3, 4, x) with a few nuclei. Similar structures are referred to as "organs of problematic nature" by Goto (1895:103) in *Epibdella ovata*, and by Cooper (1921:5) in *E. hippoglossi* (Müller 1776) simply as "polynucleate giant cells." Goto states that they are composed of a mass of polygonal cells, each with a nucleus, but in *Megalocotyle marginata* the organ seems to be polynucleate, and devoid of any cell walls, except in investing membrane. Heath (1902:117) describes two pairs of such cells in *E. squamula*. In no case has any function been ascribed to these bodies.

Female: The ovary (figs. 2, 3, o) is situated in the median line just anterior to the testes, and is midway between the dorsal and ventral walls of the body. It is globular in form, with an indefinite formative region, altho the mature ova are usually found in the central and anterior portions of the ovary. The oviduct (fig. 8, od) arises from the dorsal side of the anterior end of the ovary. Almost at its origin it unites with the unpaired yolk duct (fig. 8, vc) arising from the dorsal surface of the yolk reservoir. It proceeds cephalad, first turning slightly to the left, then to the right, until it reaches an ovoid body (fig. 8, po) slightly smaller than the prostate gland, which it enters dorsally near the posterior end. This structure is composed of mesenchyme and a small amount of connective tissue. The oviduct then proceeds anteriorly, imbedded in this tissue, until it reaches the level of the posterior end of the seminal receptacle. Here it emerges on the ventral side, the thin wall then becoming very thick, and turns sharply posteriorly and again extends forward, thus

forming a U on the under side, the distal end of which connects with the ootype. No organ of the type mentioned above (fig. 8, po), just posterior to the ootype, has been described for any other genus in the family Tristomidae. Heath (1902: fig. 11, pl. 16) figures a structure around the anterior end of the oviduct, but makes no mention of it in his description of *Epibdella squamula*. It has no apparent function unless it might be that of a pulsating organ to aid in forcing the various components of the egg into the ootype. However, the cells making up the organ are almost entirely mesenchymous rather than muscular, which one would expect if its main purpose is pulsation. Shell gland ducts (fig. 8, sd) may be found entering the oviduct on the dorsal side of the "pulsating organ" and in the median line of the body. At the end of each duct is a unicellular shell gland (fig. 8, sg). The ducts are readily found in sectioned mature worms, since they stain heavily with haematoxylin. Beyond the shell glands the oviduct enters a heavy-walled, pearshaped ootype (figs. 2, 8, ot) and from this a short uterus (figs. 2, 8, u) leads into the genital atrium (figs. 2, 8, ga) at a point about one-third the breadth of the worm from the margin. Vitellaria (fig. 3, vi) occupy all the space lateral to and behind the genital organs, except a small area in the posterior end. Anteriorly the vitellaria on the right extend to the anterior sucker, but on the left they reach only to the common genital duct. The yolk glands are closely crowded leaving only a very thin layer of mesenchyme between them (fig. 4). Paired yolk ducts unite in front of and slightly ventral to the ovary (fig. 2, vc2) to form a yolk reservoir on the right of the median lines (fig. 2, vr). From its dorsal side a short unpaired yolk duct (fig. 8, vc) joins the oviduct. An unpaired vagina (figs. 2, 8, va) arises from the anterior surface of the yolk reservoir and proceeds to the exterior on the left of the female ducts and parallel to them. It is enlarged into a heavy walled pyriform seminal receptacle (figs. 2, 8, sr) at the level of the ootype. The vaginal opening (fig. 2, vp) is on the lateral margin immediately behind the common genital pore. The stalked tetrahedral eggs are laid singly (fig. 5).

DISCUSSION

In many respects the new genus resembles certain forms of other genera of the same family. The organs of attachment suggest *Tristomum*, and the general arrangement of the genital system is similar to that of *Epibdella*, especially *E. scianeae* (P. J. v. Beneden, according to Goto, 1895:269). However, there are some very outstanding differences.

Tristomum possesses scattered testes whereas in *Megalocotyle* there are only two. Furthermore, the posterior margin of the body is notched in *Tristomum* and the fixation disc is comparatively small, while in the new genus the body is not notched but becomes gradually narrower and is directly continued into the sucker, which is in every case as broad as the body. The arrangement of septa in the posterior disc is also different in the two genera. In *Tristomum* the septa form a heptagonal central area, while in *Megalocotyle* they form a pentagon.

The most striking distinction between *Megalocotyle* and *Epibdella* lies in the posterior sucker. This organ bears no septa in *Epibdella*, and carries a simple marginal membrane. The fixation disc of *Megalocotyle* is traversed by a regular number of raised septa and its membrane is thrown into wavy folds. However, this latter point may be merely a specific characteristic.

Since the trematode herein described is unlike any other of the family *Tristomidae* in its type of posterior sucker and in the possession of two testes, it is referred to a new genus.

MEGALOCOTYLE MARGINATA

as - anterior sucker	po - problematic group of cells, "pulsating organ"
b - brain	pr - prostate gland
c - semicircular commissure	ps - posterior sucker
ce - eyespot	sa - salivary glands
cp - excretory pore	sr - seminal receptacle
er - excretory reservoir	t - testes
ga - genital atrium	u - uterus
gp - genital pore	va - vagina
m - mouth	ve2 - paired vitelline canal
me - mesenchyme	vd - vas deferens
o - ovary	vi, vit - vitellaria
od - oviduct	vn - ventral nerve
oe - oesophagus	vp - vaginal pore
ot - ootype	vr - vitelline reservoir
pd - duct of prostate gland	x - problematic organs
ph - pharynx	

Fig. 1. Brain. From a reconstruction of frontal sections. $\times 55$.

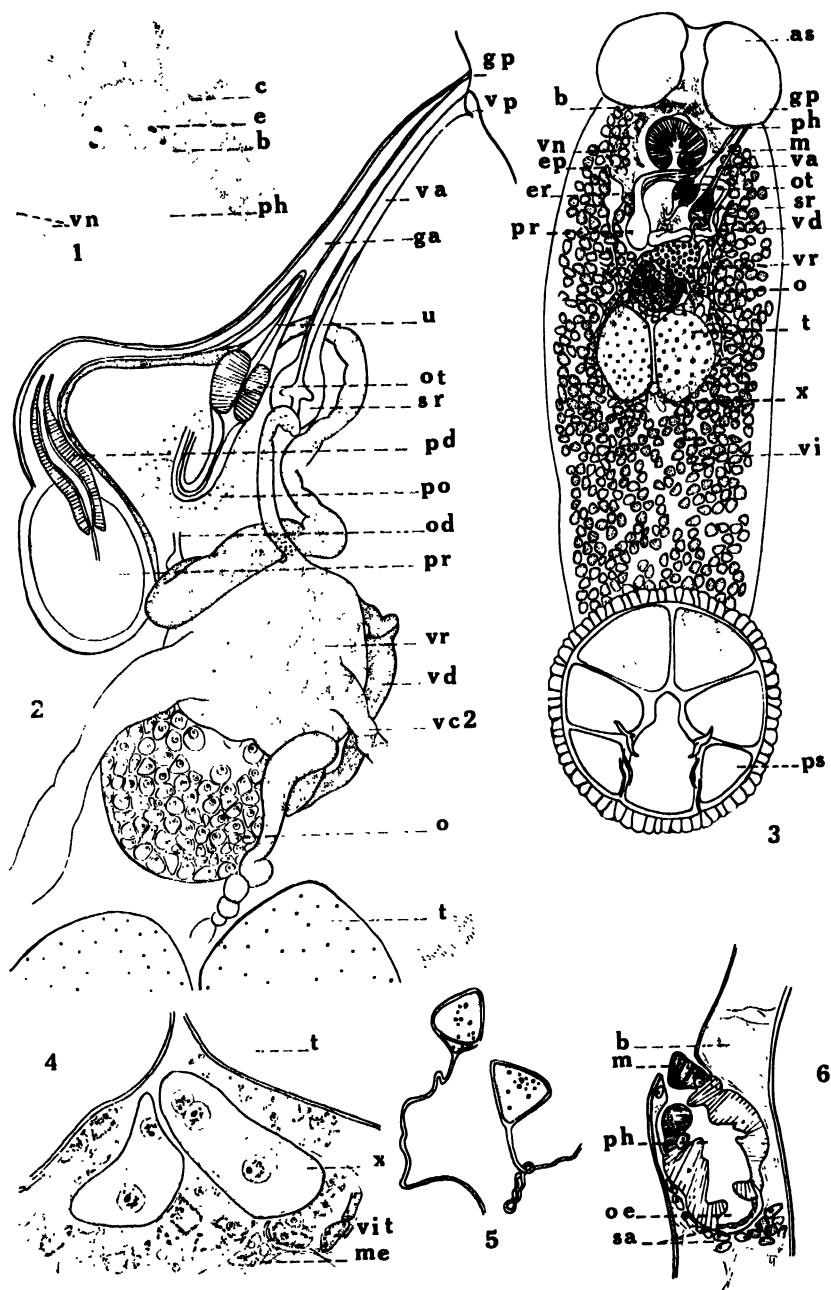
Fig. 2. Reproductive system, ventral view; from whole mount and living specimen. $\times 130$.

Fig. 3. Ventral view of entire worm, 1.9×0.58 mm; from whole mount. $\times 55$.

Fig. 4. Problematic organs lying posterior to testes; from a frontal section. $\times 275$.

Fig. 5. Two mature eggs laid in dish. $\times 55$.

Fig. 6. Pharynx, sagittal section. $\times 65$.



MEGALOCOTYLE MARGINATA

MEGALOCOTYLE MARGINATA

c - chitinous piece	po - problematic group of cells, "pulsating organ"
er - excretory reservoir	pr - prostate gland
ga - genital atrium	s - septum
gp - genital pore	sa - salivary glands
i - intestine	sd - shell gland ducts
m - mouth	sg - shell glands
mm - marginal membrane	sr - seminal receptacle
o - ovary	u - uterus
od - oviduct	va - vagina
ot - ootype	vd - vas deferens
p - penis	vc - unpaired vitelline canal
ph - pharynx	

Fig. 7. Dorsal view of entire worm, 1.9×0.58 mm; from whole mount. ×55.

Fig. 8. Reproductive system, dorsal view; from whole mount and living specimen. ×130.

Fig. 9. Posterior sucking disc, ventral view; from whole mount. ×130.

Fig. 10. Hooks on right septum, ventral view; from whole mount. ×185.

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Nereocystis

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INTRODUCTION

For the last few years botanists who have been keenly interested in the algae have had their attention largely centered on the Phaeophyceae. Part of this group, the Laminariales, altho having some of the characteristics of the higher plants, has long been looked upon as having a rather primitive life history.

Drew¹ in 1910 reported fusion of motile gametes of *Laminaria*, figured resulting plants and described their growth. Williams² in 1913 repeated the experiments of Drew. His observations did not quite coincide with those of Drew in that he did not find the fusion of the motile spores, produced by the large *Laminaria* generation. He concluded that the colorless fusing bodies that Drew described were not spores of the plant in question. He calls these bodies monads. Williams also described the young plant resulting from the *Laminaria* spores together with a subsequent development from an extruded cell of a more complex body, which he calls a germling.

It remained for Sauvageau³ in 1916 to interpret these facts thru his cultural study of another genus, *Saccorhiza bulbosa*. He reported a differentiation in the little sporelings and called them male and female gametophytes. The extruded cell which Williams had observed in *Laminaria* was present here and gave rise to a plant similar to that described by Williams. Sauvageau rightly conceived this extruded cell to be the egg, and the small plant resulting from it to be the sporophyte. He decided that the other small cells (often empty) developing on the smaller, less complex plant, were antheridia. He followed this study in 1916 with like observations on *Laminaria*

¹ Drew, G. H. The reproduction and early development of *Laminaria digitata* and *Laminaria saccharina*. Ann. Bot. 24:177-190. 1910.

² Williams, J. Lloyd. The zoospores of Laminariaceae and their germination. Rept. 82. Meeting of British Assn. Adv. Sci., Dundee. 1912.

³ Sauvageau, C. Sur la sexualité heterogamique d'une Laminaire (*Saccorhiza bulbosa*). Compt. Rend. Acad. Sci. Paris 161:746-799. 1915.

saccharina, *L. flexicaulis*⁴ and *Alaria esculenta*.⁵ Kylin⁶ in the same year confirmed Sauvageau's observations in his study of *Laminaria digitata* (*L. flexicaulis*), and in 1918⁷ summed up the facts concerning the alternation of generations in the Phaeophyceae, giving a comprehensive bibliography.

In a preliminary paper in 1921 Williams⁸ completed the chain of evidence for alternation of generations thru the discovery of the free sperms and the fertilization of the egg in *Laminaria* and *Chorda*. Thus the conception of this great group was changed and alternation of generations became a firmly established fact.

Myers⁹ in 1925 published the life history of *Postelsia palmaeformis* and of *Laminaria sinclairii*, and in 1928¹⁰ that of *Egregia menziesii*. In the latter paper she established alternation of generation by chromosome count. Delf and Levyn¹¹ in 1926 published a report on alternation of generations in *Macrocystis pyrifera*, and Angst¹² in 1927 described it in the development of *Costaria costata*. The life histories of the closely related genera are still only conjectural.

The purpose of this paper is to gather the existing literature on *Nereocystis luetkeana* (Mertens) Postels & Ruprecht, and to set forth its life history as determined by cultural methods.

HISTORY

Nereocystis luetkeana, the only species of the genus, was first described by Mertens (1820), under the name *Fucus lütkeana*; however, Setchell (1908) refers to a rare edition of Maurelle's "Journal of a voyage in 1775 to explore the coast of America northward from California." This author tells of a floating sea weed, the description of which answers to that of *Nereocystis*. As the latitude and longi-

⁴ Sauvageau, C. Sur les gametophytes de deux Laminaires (*L. flexicaulis* et *L. saccharina*). Compt. Rend. Acad. Sci. Paris 162:601-604. 1916.

⁵ Sauvageau, C. Sur la sexualité heterogamique d'une Laminare (*Alaria esculenta*). Compt. Rend. Acad. Sci. Paris 162:840-842. 1916.

⁶ Kylin, H. Ueber den Generationswechsel bei *Laminaria digitata*. Svensk Bot. Tids. 10:551-561. 1916.

⁷ Kylin, H. Studien ueber die Entwicklungsgeschichte die Phaeophyceen. Svensk. Bot. Tids. 12:1-64. 1918.

⁸ Williams, J. L. The gametophyte and fertilization of *Laminaria* and *Corda*. (Preliminary account). Ann. Bot. 35:603-608. 1921.

⁹ Myers, M. E. Contributions toward a knowledge of the life histories of the Melanophyceae. (A preliminary report). Univ. Calif. Pub. Bot. 13:100-124. 1925.

¹⁰ Myers, M. E. The life history of the brown alga, *Egregia menziesii*. Univ. Calif. Pub. Bot. 14:225-246. 1928.

¹¹ Delf, R. M. and Levyn, M. Reproduction in *Macrocystis pyrifera*. Ag. Ann. Bot. 40:503-506. 1926.

¹² Angst, L. Gametophytes of *Costaria costata*. Pub. Puget Sound Biol. Sta. 5:293-308. 1927.

tude was that of the Alaskan coast, it is very probable that he was describing the *Nereocystis* beds.

Postels and Ruprecht (1840) first described the plant under the name *Nereocystis lütkeana*. Harvey (1852) refers to *Nereocystis*, giving Mertens' description in full, and adds that the plant seems to be confined to "Russian America." Areschoug (1876) contains the first description of the fruiting structures and the young plants. Macmillan (1899) added to this knowledge of the young plants when he examined hundreds of *Nereocystis* plants from a collection made by Tilden at low tide at a depth 60 cm. He states that the series "includes undoubted specimens from $\frac{1}{2}$ mm in length to 80 feet" (25 meters).

From this time *Nereocystis* has been the subject of many papers. Its abundance and possible utilization as a source of potassium salts and iodine has led to investigations by individuals and governments to determine its value and the extent of its beds. In the bibliography given at the conclusion the writer has endeavored to include all papers resulting from such investigations as well as those of purely scientific purport.

Cultural work on the problem was begun by the writer in 1925 and repeated in 1925-1926 with some success, but the slow growth of the young gametophytes, the absence of good working conditions, and the distance from the *Nereocystis* beds, made the problem a difficult one. In 1927 cultures were set up at the Puget Sound Biological Station under more favorable conditions. The results of the combined data from all of these experiments form the basis of this paper.

GENERAL DESCRIPTION

Nereocystis grows only in the Pacific Ocean off the coast of North America. Jordan (1896-1897) in speaking of the range of the plant says, "It certainly extends as far north as Unalaska and may very likely range as far up as the Pribilof group." Setchell (1912) gives as its range, Point conception, California to the Shumagin Islands, Alaska. The beds vary in size and somewhat in location from year to year. The bed at Lincoln Beach, Seattle, from which most of the material was collected during the winters of 1924-1926, has been described by Rigg (1915a). This bed is not so extensive as some of those in the neighborhood of the San Juan Islands, but at all times supplied reproductive material for the setting up of the cultures. In the period from February to the last of May reproductive

material was not abundant, since most of the plants disappeared during the winter months.

The adult sporophyte consists of a complex holdfast made up of branching, intertwined hapteres and a long stipe topped by a hollow bulb from which the numerous fronds arise dichotomously. The fronds vary in length and number according to age.

When the fronds are mature they contain areas which have a thicker, heavier, more leathery appearance than that of the rest of the plant. As these patches near maturity, they become quite noticeable, varying in size from 2.5-10 cm in width and often reaching a length of 45 cm. These are the fruiting areas. They may be found in a series on the same frond, from those which are just forming and scarcely discernable to those mature, dark, olivaceous ones which are ready to shed. The older ones are nearer the tip of the frond; when the zoospores are mature the patch separates from the frond, leaving a hole. The frond is thus weakened by perforations, and becomes ragged and frayed by action of wind, waves and tide.

By the first of April small plants with fronds a meter long may be found in the edge of the water just beyond low tide. Plants of all sizes from a centimeter up may be collected at this time.

As the plants near the shore are mixed with *Laminaria* and other large browns, one cannot be sure of their identity, at least by macroscopic observation, until they have reached a length of about 10 cm. At this time the stipe has become one-third the length of the whole plant; the little lines along which the frond splits some time later have begun to be evident, and a slight bulge in the stipe indicates that the pneumatocyst is forming.

In artificial cultures sporophytes reached a length of 1.5 cm in 10 months from the time when the first sporophyte appeared. Their growth was probably retarded by the confines of the dish, their too great abundance in the cultures, together with other conditions not met with in nature. Of course, growth cannot be so rapid at this stage, as in later stages when the cells number many times those of the small plant.

The *Nereocystis* plant, when full grown, varies in size according to the depth from which it comes and according to other determining factors of which Setchell (1912) and Rigg (1913) conclude salinity to be one. Frye, Rigg and Crandall (1915) found them reaching a total length of 38.4 meters, and growing at a depth of 17 meters.

The length of the life of *Nereocystis* is still uncertain but the slow growth of the gametophyte, its age at maturity, and the subsequent slow growth of the sporophyte in cultures has led the writer to agree with Frye (1906), who suggests that *Nereocystis* may not reach the surface the first year.

METHODS OF CULTURE

The culture solutions were all made on the same general plan. In each dish was placed .5-1 liter of sea water to which had been added sodium nitrate in the ratio of one gram per liter and a crystal of potassium phosphate about half the size of a grain of wheat. The sea water was either filtered or sterilized; if sterilized it was placed in an autoclave or pressure cooker, brought to 10 pounds pressure and left for 20 minutes; if filtered, it was run thru a fine filter several successive times in order to remove everything that might interfere with the clearness of the cultures.

Cultures set up with sterile sea water were freer of bacteria, diatoms, plant and animal life, and this method was therefore used in all the later experiments. Slight variations in the amount of sodium nitrate showed that in .1% to .15% solutions the plant growth was fairly constant. Where less than .1% was used the cells of the gametophyte were spherical, quite uniform in size, and the filaments did not grow rapidly or branch. Slight variations occurred in some of the other solutions, but because so many factors are encountered in general cultures, no conclusions could be drawn.

As the .1% sodium nitrate solution used by Kylin on *Laminaria* seemed to be favorable for the growth of the small *Nereocystis* gametophytes, this amount was used in all the later cultures. Acme section jars were chosen for the experiments, as these could be placed one above the other. However, the method of placing them one above the other was early given up when it was found that the cultures did not thrive so well as when surrounded by a greater amount of air. In order to increase the amount of air after sterilization, the water was poured back and forth several times from a height of 20-30 cm. As many slides as could be accommodated were then placed on the bottom and around the sides of the dishes.

When the solutions were in readiness, trips were made to the *Nereocystis* beds. During the winter of 1924-1925 and that of 1925-1926, all material was collected from Lincoln Beach which lies about ten miles from the University of Washington campus. During the

summer of 1927 at the Puget Sound Biological Station, the reproductive portions of the fronds were obtained from a small bed off Point Caution, about a quarter of a mile from the Station float. Since plants nearer the shore were covered with dense growths of *Ectocarpus*, the material was taken, for the most part, from plants that grew in deep water.

The reproductive parts were collected just as they were dropping from the blades and brought to the laboratory in plenty of fresh sea water. Pieces .5-1 cm square were cut, washed several times in filtered or sterile water and placed in the culture solutions previously described. Only three or four pieces of this size were placed in each dish. Small pieces and large amounts of solution were used, that the danger of contamination by other filamentous brown algae might be minimized. So thoroly was the washing done that cultures practically pure, except for protozoans and bacteria, were secured.

In 1924-1925 the cultures were then placed out-of-doors and covered in such a manner that they were protected from dust and at the same time were constantly supplied with fresh air. To accomplish this the dishes were placed on an open grating and covered with a large bell jar. Cultures set up in this way in September usually died because at that time the temperature varied too greatly. For this reason cultures were set up at intervals of a week or two weeks until the first of December.

In 1927 at the Biological Station, the temperature was more easily regulated. The dishes were placed in a shallow cement tray and surrounded with sea water conveyed to the laboratory from a storage tank by a pipe that runs for some distance thru the cold water of Puget Sound. A faucet above the tray supplies the inflow; the outlet allows for the control of the depth of water in the tray. The water was maintained at a fairly constant temperature. At no time did it register higher than 18°C. with an average of about 16°C. The pieces of reproductive material in the cultures were removed after 12 hours. By this time enough zoospores had liberated themselves to make a thin brown film on the top of the water in the dishes. A drop of water on a slide showed myriads of tiny brown moving forms.

Permanent slides were then made by placing a drop of the solution on a slide, putting the slide over osmic acid in a closed container, leaving it for five minutes and then drying the slide slowly in the air. The carbol-fuchsin method was used in the staining. This

gave the chromatophores, together with the cilia of the zoospores, a bright red color, and stained but slightly the wall and protoplasmic contents.

The zoospores as seen from a stained prepared slide were ovoid with a slight depression on the side nearer the smaller end, from which depressions arose two cilia of unequal length, the shorter one being about the length of the spore itself, the other twice the length (fig. 1). The body of the zoospore measured 3.8-4.2 micra in length, by 1.5-3.1 micra in width. It contained one large, rather irregular chromatophore parietally located near the smaller end of the spore.

The zoospores in fresh cultures swam about quite actively for a short time, then rounded up and provided themselves with a wall. They settled on the slides, on the bottom or sides of the dishes, or floated in great numbers on the surface of the water. They adhered closely in groups when in this floating condition.

GAMETOPHYTE

In 24 hours after the reproductive material was placed in the dishes many of the small spores began to germinate by putting out a short projection. The tube which formed from this was much smaller in diameter than the spore itself. By the second day most of the contents of the cell had pushed into the filament thus formed, and the end had swelled, giving the whole the appearance of a tiny dumb-bell, similar to that shown in drawings for other genera of the Laminariaceae by Sauvageau and others (figs. 4, 5, 6). Soon, with the exception of a small amount of protoplasm, the contents of the spore became the contents of the swollen end. This now formed a wall and the first cell of the young gametophyte was completed (fig. 7). At this stage the cell had two or more chromatophores.

For several days the cell increased in diameter and in number of chromatophores. It then started to grow by a process similar to that seen in the spore except that the contents of the cell became dense and remained so. The filament instead of rounding up at the end remained the same diameter and the first cell divided it into two almost equal parts (fig. 14); at about the same time a wall appeared separating the basal portion from the filament of two cells, thus forming a three-celled gametophyte (figs. 20, 21, 22). The division of the cells in the filament continued. Up to the time that the filament was 6-8-celled the cell division caused increase in length only,

and this growth in length was entirely in cells other than the basal. This cell, however, then rounded up, increased in size until its diameter was 1.5 times that of the filament. It sometimes divided and formed a wall diagonal in direction to those in the filament. The first division of the basal cell was often unequal. At right angles to the diagonal wall might appear another wall in the larger cell. Subsequent cell division created a mass of cells from each of which a branch might be sent out, giving the whole a rosetted appearance (fig. 48). At other times the basal cell just remained a noticeably larger cell and the cells in the filaments sent out branches. Often all the cells in the filaments formed branches. These branches were at times all on one side, at other times some on one side and some on the other; again there was only an occasional branch in the whole gametophyte.

In some cases all of the cells in a gametophyte died but one. That one might increase in size and number of chromatophores and then give rise to a new plant dense with protoplasm and brown in color. The cause of the death of the filament or of the rejuvenation of the plant by the remaining cell was not apparent, altho this was a common occurrence in cultures that were otherwise seemingly healthy. At the time the cultures were 3-4 weeks old, the sides and bottoms of the dishes were brown with the growth. The surface had a thick, brown film which, when viewed under the microscope, was seen to be composed of sturdy plant filaments. They seemed to thrive equally well in all parts of the dishes.

In cultures 3 weeks old there was still belated germination of the asexual spores (fig. 18), suggesting that perhaps these heavier structures had resulted from spores that had a longer maturation period. From time to time cultures that seemed to be laboring under adverse conditions degenerated into filaments of rounded cells with slightly heavier walls. In these cultures but little branching was seen.

The slides in the bottoms of the dishes were removed from time to time and made into permanent mounts. The small plants adhered so firmly to the slides that they could be killed and run thru the different staining processes without being loosened. At the end of 4 weeks the slides had such a growth of young plants that together with the debris that collected from different sources they were not worth much as permanent slides. From this time forth, if the material was desired for permanent mounts, it had to be treated in another manner.

Very little differentiation of the plants was noted before they were 9 or 10 weeks old. Then some of the plants became noticeably stouter in cell structure, more complex in their branching, denser in protoplasm and chromatophores and correspondingly darker brown in color.

Cultures set up by Myers in 1924, but abandoned at the end of the summer, were still growing in 1925. They were again supplied with sterile water and nutrient salts, and left until the next summer. They were still living in the gametophyte stage in the early part of the summer of 1928. Each summer they were taken care of in the same way. No attention was paid to the temperature, and the air space left in the dishes was small. These cultures showed two differentiated structures. One consisted of small round cells, as was the case also in some of the writer's cultures. The other was an unbranched, very much smaller filament with slightly longer cells, which was somewhat similar to the male gametophyte in some of the cultures set up by the writer. There were no sporophyte structures in the Myers cultures and care during the summer of 1927 and thruout the year until 1928 did not produce any, at least not in the 9 weeks that they were under observation each summer. At the end of the summer in 1928, after being carefully nourished and kept at the constant temperature, as were my own cultures, the cells had taken on the dark brown coloration and were much the same in appearance as the gametophytes in cultures that were producing fruiting bodies.

Cultures set up on July 1st, 1927 at the Puget Sound Biological Station had not produced oogonia or antheridia when the time came to leave the Station, so they were left in the care of Martin Johnson, the curator, to collect and send samples to the writer at the University of Washington. The samples of the 11th of September contained the fruiting structures, exhibiting the quite apparent differentiation of the two gametophytes.

FEMALE GAMETOPHYTE

This differentiation showed in the size and to some extent in the color of the filaments. Some of them had taken on a sturdiness of form not so apparent in the earlier structures. These gametophytes had increased in diameter, and were a richer brown in color due to the increased numbers of chromatophores. The walls of the cells had a somewhat heavier appearance. The apical cells of many of the branches were several shades darker than the rest of the filament.

Their length was much augmented and the apex of the cell was decidedly swollen. This made the oogonial structures, as these later proved to be, strikingly noticeable. From the ends of several empty cells in this culture 1- or 2-celled sporophytes could be seen dotting the cultures here and there.

In observations on previous cultures and on these cultures in a live state in the summer of 1928, the writer often saw the oogonial cell empty its contents. The cell when mature had its contents crowded into the apex. Behind and around this contents the cell was filled with a dense colorless substance. The cell broke at the tip and the mass of material contained in it moved out into the surrounding water. As early as 1916 both Sauvageau and Kylin observed the same phenomenon in *Laminaria*. This extruded cell seemed to have a membrane surrounding it, for after flowing out thru the small opening, it immediately rounded, adhering closely to the empty oogonium. It then formed a cell wall about itself and began to elongate. The fertilization has not been observed nor has cytological work been done on the plant.

In older cultures oogonia occurred not only in the tip cells of the branches; any cell of the filament might elongate at right angles to the main axis and become an oogonium. As the cultures grew older, all the cells of the female gametophyte took on the dense brown color, and the oogonium was less distinctly noticeable than in the younger cultures. By the time the oogonia were formed the gametophyte was an elongated and much branched structure, or had become a decidedly resettled structure with many branches (fig. 48), the tips of which produced the oogonia. One plant could give rise to many sporophytes and as the plant could reproduce vegetatively from a singly cell, limitations on sporophyte production did not seem to exist.

When the cultures had been newly supplied with much nutritive solution, or continuously supplied with fresh sea water from the tap, an interesting development occurred in older cultures of the gametophyte. This was the formation within the filaments of giant cells 140 by 45 micra. These giant cells in some cases just died without much change; sometimes they sent out 1 or 2 thrifty branches from their sides; and at other times they divided into many cells, forming plate-like structures the branching of which produced rosettes of filaments from common centers, similar to those made by the division of the basal cells of the gametophytes.

MALE GAMETOPHYTE

Very intimately associated with the above sturdy, coarse filaments were plants much more delicate in appearance. They were paler in color, contained the same type of laterally placed chromatophores, had the same kind of branching filaments and became very extensive before they began to be interesting in a reproductive way.

At first the antheridia were formed at the tips of the branches and consisted of finger-like projections rounding out from much divided and plate-like or spherical structures formed from many divisions of the apical cells (figs. 40, 41). The contents of the outermost cells then rounded up and produced single sperms. This seemed to be the condition as observed in most of the Laminariaceae.

The whole much-branched antheridial portions of the male gametophytes gradually emptied as the cells successively produced sperms and the latter escaped. The escape was not observed; therefore, whether the forms which emerged were free-swimming is still to be determined. The evidences that there were sperms were the presence in the cultures of the antheridial structures, the single small bodies in the cells, and then the empty cells after the sperms had abandoned them. Observations by writers on other genera also led to this conclusion.

SPOROPHYTE

The sporophytes began to appear when the cultures were between 10 and 11 weeks old. After the egg left the oogonium it rounded up. A wall formed about it and it began to grow. The first indication of growth was the elongation of the cell to almost twice its former length (fig. 42d), after which a wall appeared at right angles to its main axis, dividing it into two either equal or unequal parts. If unequal, the larger part was usually the basal cell. The tip cell was the one to divide first; the two resulting cells each divided again or only one divided. In one case the young sporophyte consisted of 5 cells, in the other of 4 cells; both conditions were found. The basal cell continued to grow. Most of its chloroplasts were grouped in the upper part of the cell. It then divided, leaving the lower cell without many chloroplasts. This cell then began to push downward at one side, becoming the first rhizoidal cell. It was not until the sporophyte was 6- to 12-celled that the cells began to divide in another direction. Those in the center of the plant were the first to divide vertically, thus causing the widening of the sporophyte just above the middle.

With *Egregia*, Myers reported the first vertical division taking place in the apical cell. In *Nereocystis* the apical cell did not divide until several of the central cells had divided.

The small plant was monostromatic until it had 40-50 cells; then the cells at the base began to divide in a third plane. Each of the basal cells sent down a rhizoid until there was a tangled mass. Where these rhizoids came in contact with the walls or sides of the dish they flattened slightly at the ends; sometimes they forked there. The monostromatic character of the few cells at the tip of the plant seemed to remain for some time; this part then died. The basal portion, which was then composed of several thicknesses of cells, formed a new tip not so acute as the old one.

When the small sporophyte was .5 mm long, the large cells of the inner web which gave rise to the sieve tubes were already formed. Some of them measured 141 by 45 micra; others were 45 micra square; and the surface cells in the rapidly dividing cortical areas were but 24.9 by 13 micra, to about 13 micra square. Sporophytes 1.5 cm long were found in cultures that were a year old. At this time the basal portion had become a decidedly conical disk; the stipe was apparent and the edges of the disk showed slight projections. The earliest signs of these projections were the pushing out of cells in certain regions beyond the border of the disk. These cells were quite evident in the early formation of the disk. The resulting crenate appearance in the slightly older disks seemed to be the result of apical growth from these cells. By the time the disk and its protuberances were well formed, the abundant rhizoids which had grown out from many of the surface cells and formed an intertwined mass, had disappeared. The rhizoids, as reported by Myers for *Egregia*, were without transverse walls and were unbranched, except for the above mentioned somewhat forked condition when they came in contact with the slides or sides of the dishes. Angst, however, reported cross walls in the rhizoids of *Costaria*. The small sporophytes grown in cultures as well as those collected in nature showed, upon microscopic examination of the surface, decided lines thru the frond emerging from the top of the stipe and radiating out fan-shaped thru the frond. These lines had the appearance of long inner web cells reaching the surface along certain lines and not covered with the smaller cortical cells.

In a cross section thru the small disk holdfast and thru one of the protuberances, the disk was seen as a solid growth of cells, of which only the outer ones had chromatophores. The inner colorless

ones from the crenate portion of the disk were elongated toward the center of the disk. A cross section above the basal portion showed the colorless cells to be iso-diametric. The hapteres are a later development, and to date have not appeared. It is probable, however, that these are formed in much the same way as the crenate margins of the disk.

On the whole *Nereocystis* differs from the Laminariaceae that have been previously described in that it has a gametophyte growth of much longer duration before maturation, and that its antheridial gametophyte is much more branched and extensive than those described for the other forms. It has an indefinite reproductive period. That the gametophyte can live thru several years has not been tested for others of the group.

SUMMARY

Nereocystis has differentiated male and female gametophytes with much branched and extensive filaments. The gametophyte plant has the power of vegetative reproduction and of continuing its reproductive processes for at least a year.

The gametophyte takes between 10 and 11 weeks to reach maturity.

Cultural sporophytes have been grown to 1.5 cm in length and have developed a primary disk, a holdfast, stipe, and frond which lost its monostromatic character.

Summary of Process of Growth

24 hours; spores started germinating.

48 hours; cell contents passed into the new ends of the filament.

1 week; gametophytes of 2 cells.

2 weeks; gametophytes of 3 cells.

3 weeks; gametophytes of 4-8 cells; one or two individuals started to extend cells laterally as in branching.

4 weeks; plants showed many cells and more branching.

5 weeks; many branches present; basal cells of the gametophytes began to divide and branch.

6 weeks; filaments were still lengthening and branching profusely.

7-8 weeks; filaments were becoming complex, almost plate-like in some cases; differentiation of gametophytes became apparent.

9 weeks; sexual differentiation was more decided.

10-11 weeks; oogonia and antheridia present; sporophytes began to appear.

12 months; sporophytes were still forming; all stages of growth were found in the cultures.

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Fig. 1. Zoospores. $\times 650$.

Fig. 2. Germinating spore. $\times 650$.

Fig. 3-7. Stages in the germination of the spore, $\times 650$; x, spore end.

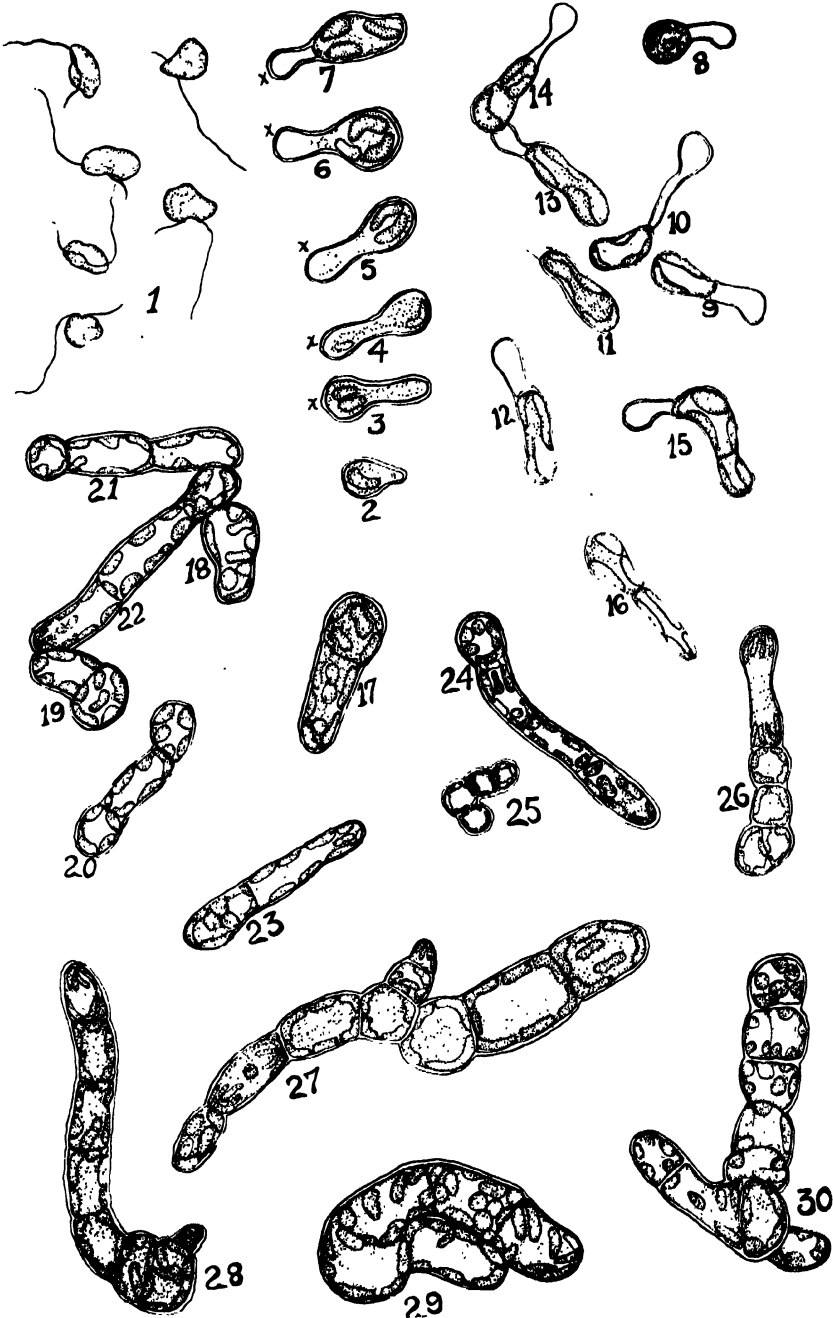
Figs. 8-13. Progressive steps in the growth of the one celled gametophyte. $\times 650$.

Figs. 14-16, 23. Two celled gametophytes. $\times 650$.

Figs. 17-23. A group of gametophytes from a three weeks culture showing various stages of germination in the same culture. $\times 650$.

Figs. 24-26. Four celled gametophytes. $\times 650$.

Figs. 27-30. Later stages in the undifferentiated gametophyte. $\times 650$.



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Figs. 31, 34. Male gametophyte when differentiation becomes apparent. $\times 650$.

Figs. 32, 35, 36, 37. Male gametophytes in the process of forming antheridia at the tip of the branches. $\times 800$.

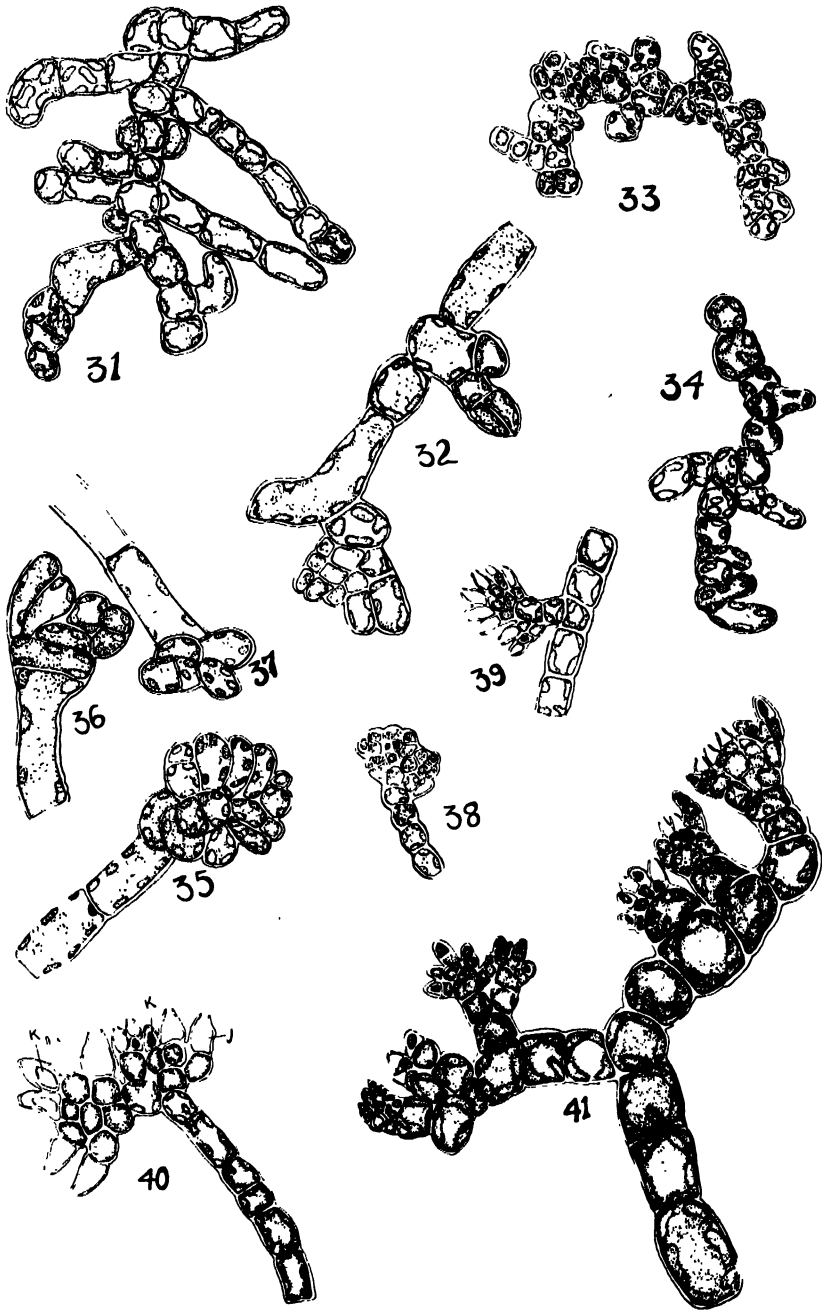
Fig. 33. Male gametophyte in older cultures, almost thalloid in appearance; each cell becoming an antheridium. $\times 650$.

Fig. 38. Antheridia forming at tip of a male gametophyte thread. $\times 650$.

Fig. 39. Antheridia forming on side branches of the male gametophyte filament. $\times 650$.

Fig. 40. Group of antheridia at tip of an antheridial filament showing (j) empty cells where sperm has escaped (k) sperms in antheridia. $\times 650$.

Fig. 41. More complex antheridial filament. $\times 800$.



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Fig. 42. Female gametophyte. $\times 250$.

a - Empty oogonium. d - Oospore.

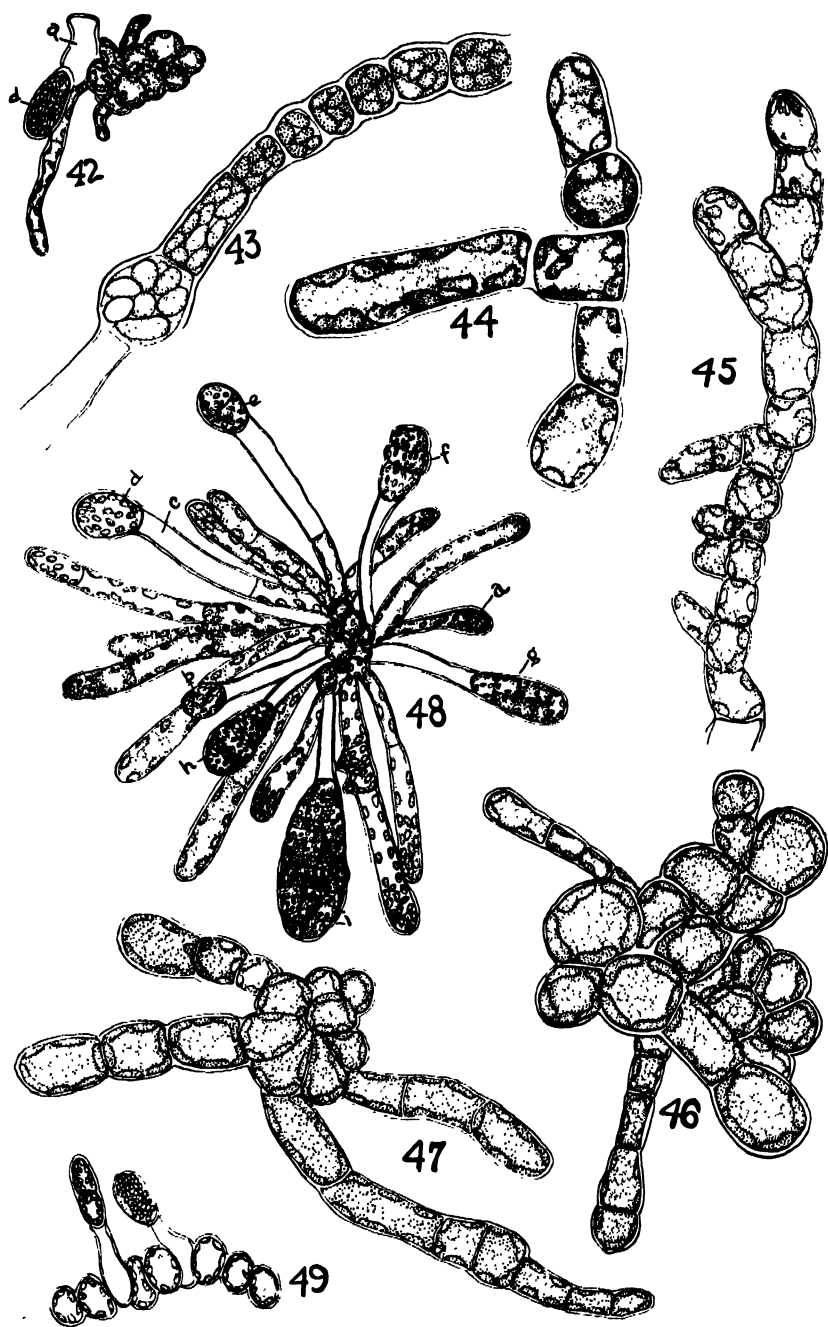
Fig. 43. Female gametophyte in older cultures when nearly every cell is spherical. $\times 650$.

Figs. 44-47. Female gametophyte at time of differentiation. $\times 650$.

Fig. 48. Female gametophyte showing the rosetted appearance. $\times 250$.

a - Oogonium d - Oospore
b - Egg e - Two celled sporophyte
c - Empty oogonium f - Three celled sporophyte
g, h, i - Various stages in the sporophyte growth

Fig. 49. Female gametophyte of older cultures. Every cell may produce a sporophyte. $\times 250$.



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Fig. 50. Portion of a female gametophyte sporophyte. $\times 250$.

a - Gametophyte

c - Sporophyte

b - Empty oogonium

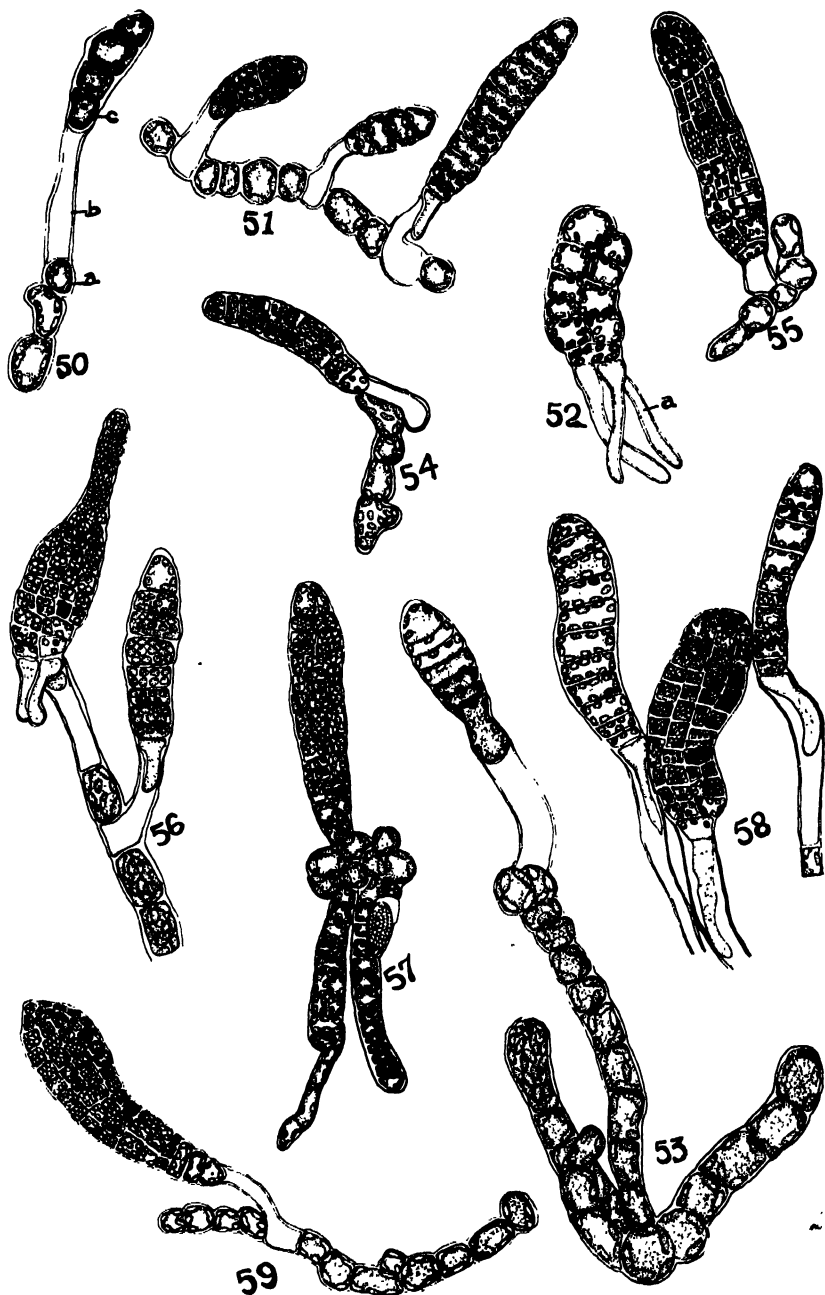
Figs. 51, 54, 55-57, 59. Female gametophytes with adherent sporophytes in various stages of development. $\times 250$.

Fig. 52. Sporophyte. $\times 650$.

a - Rhizoids

Fig. 53. Female gametophyte with sporophyte. $\times 650$.

Fig. 58. Group of sporophytes. $\times 250$.



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Fig. 60. Beginning of primary disk holdfast. $\times 250$.

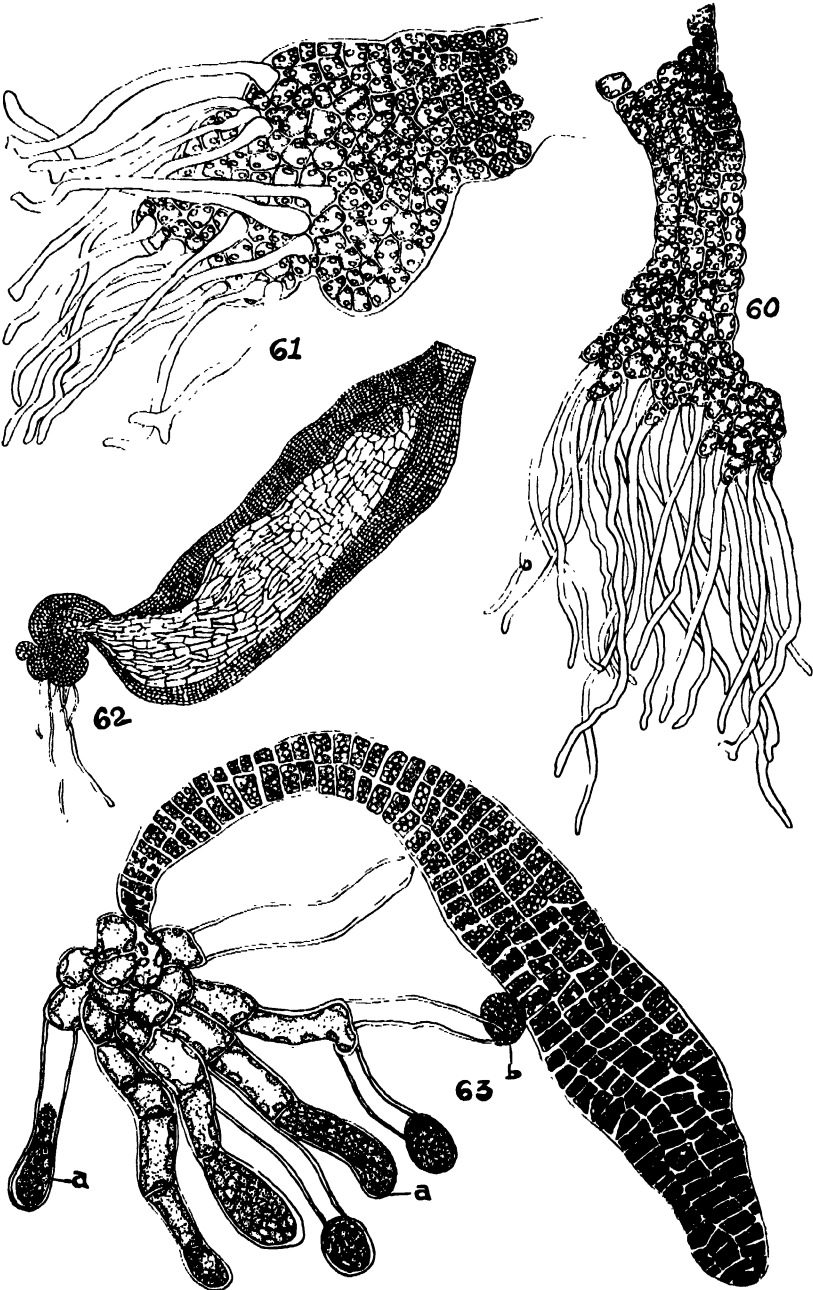
Fig. 61. Later stage in the formation of disk. $\times 250$.

Fig. 62. Plant grown in cultures (1 cm long) showing large inner web of cells and outer cortical layer of much smaller nearly isodiametric cells. $\times 90$. (Cells, in part diagrammatical).

Fig. 63. Female gametophyte with sporophyte. $\times 650$.

a - Oogonium before discharging the egg

b - Egg just after emptying from oogonium



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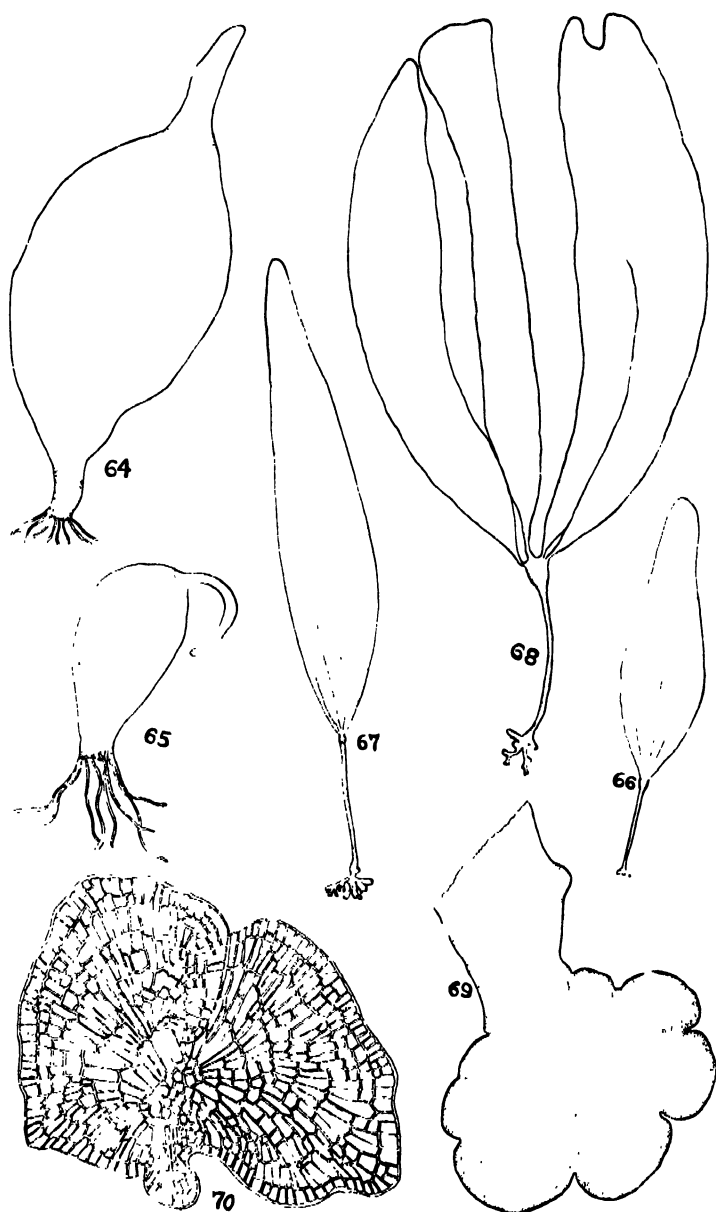
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Figs. 64-65. Outline of sporophytes. The narrower portion at tip is monostromatic. $\times 215$.

Figs. 66, 67, 68. Forms found in nature showing development of hold-fast, pneumatocyst, and splitting lines of fronds. $\frac{1}{3}$ nat. size.

Fig. 69. Primary disk on plant in year old cultures. Plant measures 1.5 cm in length. $\times 77$.

Fig. 70. Freehand section through above disk. $\times 77$.



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Fig. 71. Microphotograph of Nereocystis taken from a culture five months old. $\times 500$.

- a - Male gametophyte with antheridial cluster
- b - Sporophyte.

Fig. 72. Microphotograph of Nereocystis. $\times 500$.

- a - Antheridia shown coming from side branches in small clusters
- c - Oogonium



NEREOCYSTIS LUETKEANA

The Maturation and Segmentation of the Eggs of *Leptoplana* (sp.)¹

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INTRODUCTION

The purpose of the following study of the polyclad, *Leptoplana*, has been to discover the behavior of the eggs during their maturation, and subsequent segmentation under conditions as nearly normal as possible.

The spiral nature of the cleavage of the polyclads up to a late stage of segmentation has been demonstrated by Lang (1884) and Surface (1907), as well as by previous investigators (Girard, 1854, Keferstein, 1868, Goette, 1878, 1882, Selenka, 1881). In this respect the development of the polyclads closely resembles that of molluscan and annelidan eggs (Conklin, 1897, Mead, 1897, and Wilson, 1898). For this reason a detailed study of the behavior of the polyclad eggs in their segmentations is of interest from a phylogenetic standpoint. However, the difficulty in observing and handling the eggs, due to their opaque nature and their tough capsule or shell, thru which fixing agents and stains penetrate with difficulty, seems to have discouraged a most complete embryological investigation except in a few forms.

According to Lang, the earliest investigators of the embryology of the polyclads were Girard (1854), who described the cleavage as total and equal; Vaillant (1866, 1868), who described the segmentation into two, four and eight cells regularly arranged, but said nothing as to the size and appearance of the cells; and Keferstein (1868), who observed the extrusion of the polar bodies and described the spiral nature of the cleavage. These were followed by Hallez (1878, 1879), who held that fertilization occurs previous to the time of egg laying, and observed the giving off of the polar bodies, and one quartet of micromeres; Goette (1878, 1882a, 1882b), who also observed one quartet of micromeres; and Selenka (1881), who observed fertilization directly, and also the extrusion of the polar bodies and the formation of two quartets of micromeres.

¹Contribution from the Zoological Laboratory, Kansas State Agricultural College, No. 106, and from the Puget Sound Biological Station.

²We wish to thank Dr. J. E. Guberlet, who identified the worms.

Pereyaslawyew (1885) reported the first cleavage in *Acoela* and other forms as equal and succeeding cleavages as unequal and spiral.

Wheeler (1894) described fertilization in *Planocera inquilina* as "hypodermic impregnation." He also found that the polar bodies were extruded after the eggs were deposited.

Wilson (1894, 1898) described the cleavages as spiral and unequal.

MATERIAL AND METHODS

The material for the study of the eggs of *Leptoplana* was obtained during the months of June, July and August, 1927, at the Puget Sound Biological Station. Due to the nature of the study, practically all direct observations have been made upon the living material. The worms live in tide pools and deposit their eggs in masses on the under surfaces of small stones. During the period of high tide the pools were not exposed, thus the material could be collected only at definite times. There was no difficulty experienced in keeping the worms and egg masses in the laboratory. The sea water on them was changed once a day. In some cases the worms deposited eggs while in the laboratory, either upon stones that were kept in the jars or on the sides of the glass vessels. Observations were made on eggs laid in the laboratory and on masses brought in from the tide pools. Usually a part of a mass was removed from the stone for study, and the remainder of the mass returned to its natural habitat to be checked later.

A detailed study was made of the cleavage processes of several eggs within a mass, and later the stage of development was compared with that of eggs from the same mass which had been allowed to continue development in the natural environment. Comparisons were also made with eggs from other masses, and checked with preserved material from each mass studied. The eggs were fixed in Bouin's or Gilson's solutions. Borax carmine was used for staining. It was found necessary, however, either to remove the eggs from the capsules or to tear the capsules into pieces before the stain could penetrate to the eggs. The eggs were then dehydrated, cleared, and mounted in balsam. Serial sections of some of the eggs were made and the sections restained in Delafield's haematoxylin.

NOMENCLATURE

The system of nomenclature followed in this paper is that used by Conklin (1897) in his paper on the embryology of *Crepidula*.

The four quadrants of the egg are designated by the first four letters of the alphabet, *A*, *B*, *C* and *D*. The quartets of cells separated at various times from the macromeres are designated by small letters and coefficients; thus, the first quartet of micromeres and their derivatives are designated *1a*, *1b*, *1c*, *1d*, *1a*¹, *1b*¹, *1a*², *1b*², etc., the second quartet as *2a*, *2b*, *2c* and *2d*. The term quartet is employed as Kofoed (1894) used it to designate a group of four cells of the same generation, one of which belongs to each of the quadrants of the egg. The four macromeres are the basal quartet, the first group of micromeres separated from these the first quartet, and the second group the second quartet. The animal and vegetative poles are considered the fixed points in the egg. Of the micromeres the stem or parent cell is considered as the upper one (Conklin, 1897). If the division is to the right, that is, if the upper cell lies to the right of the lower when viewed from the animal pole, it is spoken of as dextrotropic or clockwise. If the upper cell lies to the left of the lower it is spoken of as anticlockwise or laetotropic (Lillie, 1895).

OBSERVATIONS

The worms and egg masses were found in abundance during the latter part of June and the early part of July. During the last week of July the tide pools were examined daily, as was the usual custom, but no new egg masses were discovered and the worms had entirely disappeared. Thruout August the worms were plentiful but no new egg masses were found, although the pools and stones were examined regularly.

The Egg Mass

A newly deposited egg mass is light in color in comparison with the older masses which become a dull greenish-brown color. This sometimes makes it difficult to locate the older masses on the stones. The change in color from day to day in a single mass of eggs is definitely noticeable in both the masses kept in the laboratory and those left in the tide pools.

In the laboratory, eggs were always deposited early in the morning and cleavage began a few hours later. Likewise, new egg masses were found in the tide pools only early in the morning, and in many cases cleavage had already commenced when the masses were examined.

The eggs are deposited in crust-like masses on the under surface of stones and are closely cemented to the rock. Each egg is enclosed

within an extremely tough but clear capsule or membrane. The eggs are closely but irregularly imbedded together in a single layer, so that the mass can be cut from the stone without injuring the eggs. This made it possible to watch the cleavage processes under the microscope. The main difficulty experienced in observing the cleavages of the living egg was the opacity. This was due to the amount of yolk in the egg.

The individual egg is comparatively large, spherical in shape, lies to one side of the center of the capsule, and is made up of a uniformly dense mass of granules (fig. 1). The newly laid egg is opaque, and its surface is not always smoothly round. A more or less granular substance surrounds the egg within the shell.

Cleavage occurred in a normal manner in all the masses which were laid in the laboratory except one. This one had an unusual appearance when it was deposited, and it degenerated within a few days.

Maturation

Fertilization of the egg has not been observed. Two maturation divisions occur after the egg is deposited, and two very small polar bodies are extruded and remain in contact with the egg for a while (figs. 1 and 2). The second polar body is given off soon after the first. After these polar bodies are cast off there is a noticeable clearing of the cell so that the subsequent cleavages can be easily observed. In only one case was the approximate time between the deposition of the eggs and the extrusion of the polar bodies secured, and in this, the worm was observed crawling off from a newly laid mass of eggs. Examination showed that the eggs were one-celled and opaque. Thirty minutes later, several eggs cast off the first polar body, and within a little while became much less opaque. Within two hours after the first maturation most of the cells in the mass were segmenting.

Cleavage

The cleavages in *Leptoplana* occur in intervals of approximately two and a half to three hours. About 20 minutes elapse from the time a cleavage furrow is first visible until the daughter cells are completely separated. The blastomeres rotate at the end of the segmentation, after which there is a quiescent period until the beginning of the next segmentation. Variations in the duration of these intervals were noted which may have been due to environmental conditions. In each case in which artificial light was used for observation, thus causing an increase in the temperature, the segmentations occurred

more slowly. Furthermore, development normally takes place on the under surfaces of stones, a condition in which light is largely excluded. In comparing the stage of development of these eggs which had been under observation with natural light with the remainder of the mass which had been left in the normal environment, it was found that the two were in approximately the same stage of development. Thus, temperature appeared to have a greater effect upon the eggs in their cleavages than light.

The First Cleavage. The first cleavage is polar, total, and results in two slightly unequal blastomeres (fig. 6). The egg elongates at the beginning of the segmentation. The cleavage furrow may appear first at one side of the egg, but more often it appears at both sides at the same time. The two blastomeres are at first nearly spherical, and touch each other by only a comparatively small surface (figs. 5 and 6). Later the cells are drawn toward each other, especially at the animal pole, and the surfaces of contact become much longer and flattened (fig. 7). The greater part of the yolk collects at the vegetative pole, which gives it a more dense appearance.

The Second Cleavage. The second cleavage is polar and perpendicular to the first. The cells resulting from this cleavage are also slightly unequal. The larger blastomere, *CD*, divides in advance of the other (fig. 8), often resulting in a temporary three-celled stage (figs. 9 and 10). This cleavage really consists of two independent furrows, one of them appearing earlier than the other. At the end of the cleavage the cells shift so that the two smaller cells, *B* and *D*, lie at a higher level and tend to come in contact with each other at the animal pole, forming the so-called animal polar furrow (fig. 11). The two larger blastomeres, *A* and *C*, come in contact at the vegetative pole, forming the vegetative polar furrow (fig. 12).

The Third Cleavage. At the end of the resting period the blastomeres begin to shift and lighter places appear near the centers of cells *A*, *C* and *D* (fig. 13). In a very short time these cells begin to show cleavage furrows in the equatorial plane (fig. 14). The divisions are not synchronous, as cell *D* begins to divide first; next cells *A* and *C* begin to bud off micromeres at almost the same time; and lastly, cell *B* begins to divide (figs. 14 to 17). The divisions result in two quartets of cells of decidedly unequal size (fig. 18). The basal quartet which contains the bulk of the yolk material, becomes the macromeres, *A*, *B*, *C* and *D*, and the apical quartet becomes the micromeres, *1a*, *1b*, *1c*, and *1d*. There is also a strongly dextrotropic

rotation of the micromeres during and at the close of the cleavage, as shown in figures 14 to 18, until they finally come to lie in the furrows between the macromeres. Cell $1a$ lies between A and B , $1b$ lies between B and C , $1c$ lies between C and D , and $1d$ lies between D and A (figs. 19 and 20).

The Fourth Cleavage. At the beginning of the fourth cleavage there is a further elongation of the micromeres (fig. 21) until they come to lie almost directly over their corresponding macromeres. At this stage the micromeres become exceedingly transparent, so that the egg might almost be taken for a four-celled stage when viewed from the animal pole. At the time that the micromeres begin to shift, the macromeres appear more dense near the center. Then, very quickly and simultaneously, a second quartet of micromeres, $2a$, $2b$, $2c$, and $2d$ are separated from A , B , C and D . This second quartet is slightly larger than the first quartet. The movement of this second quartet of micromeres is strongly laeotropic, so that $2a$ finally comes to lie in the furrow between A and D , $2b$ between A and B , $2c$ between B and C , and $2d$ between C and D (fig. 24).

At the same time that the macromeres are dividing, cleavage furrows appear in the first quartet of micromeres (fig. 22), and soon after the cells are completely separated, resulting in eight cells of almost equal size (fig. 24). The stem cells $1a^1$, $1b^1$, $1c^1$ and $1d^1$ shift dexiotropically, and $1a^2$, $1b^2$, $1c^2$ and $1d^2$ shift laeotropically. When the egg has passed into the resting stage the whole is very compact, with the twelve micromeres fitting closely into the furrows between their adjacent cells (fig. 24).

DISCUSSION

As has been previously stated the eggs of *Leptoplana* are made up of a uniformly dense mass of granules, and there is no differentiation into a more dense inner portion and a clearer outer portion as has been found by Selenka, Goette, Hallez, and Lang (Lang, 1884) in some polyclad eggs. Surface (1907) found the eggs of *Planocera inquilina* and Lang (1884) the eggs of *Discocoelis tigrina* to be of uniform density thruout, as are the eggs of *Leptoplana*. In *Leptoplana* never more than one egg was observed within a capsule, but Surface found that in *P. inquilina* two eggs are sometimes deposited in a single membrane, each of which develops into a normal embryo.

It is of interest to note that in *Leptoplana* the newly laid egg masses were found during only a part of the summer. This fact

tends to indicate that there might be definite reproductive periods in this particular group of *Turbellaria*.

Opinions differ as to when fertilization takes place. Lang (1884) holds that copulation occurs before egg laying but that fertilization may not have occurred by the time of the deposition of the eggs. Furthermore, according to Lang (1884), Hallez was of the opinion that fertilization occurs previous to egg laying. Lang further states that Selenka, who was able to observe fertilization in the polyclads directly, was of the opinion that the spermatozoon enters the egg and lies there until after the polar bodies are extruded. Wheeler (1894) makes this statement in regard to fertilization in *Planocera inquilina*: "There is undoubtedly in this species a true 'hypodermic impregnation', to use Professor Whitman's term. In the aquarium the sexually mature animals crawl over one another and thrust their stylet-shaped penes into one another's bodies at any point."

Although fertilization may occur previous to, or as the eggs are being deposited, the maturation divisions in *Leptoplana* do not occur until after deposition. Apparently these divisions take place soon after the egg is laid, and there is a resting period before segmentation begins. The polar bodies, which are extremely small, remain attached to the egg for a while. In other forms *Planocera inquilina* (Surface, 1907), *Thysanozoon* (Selenka, 1891) and *Discocoelis tigrina* (Lang, 1884) they do not remain attached. Surface also found that the eggs of *P. inquilina* went thru some remarkable contortions during maturation, a condition that was not observed in *Leptoplana*.

Considerable variation in the behavior of the different forms which have been studied is evident, altho they are all essentially alike. As was mentioned above, the cleavage is spiral. It is also total and unequal, and the blastomeres do not always divide simultaneously. The intervals of time between the successive cleavages also vary in different forms. In *P. inquilina*, in which the cleavages occur about every hour, the intervals are relatively short, in comparison with *Leptoplana* in which the cycle is from two and a half to three hours in length. The slower rate seems to be more constant in polyclads (Lang, 1884).

The inequality in the size of the blastomeres from the first cleavage is an outstanding characteristic of these eggs. According to Lang (1884) and Surface (1907) the difference in size of the first two blastomeres is very constant in polyclads. Lang says "Ich habe diese allerding's wenig auffallende Verschiedenheit in der Grösse der Zwei ersten Blastomeren, die Selenka bei *Thysanozoon* und *Eurylepta*

constatirte nicht nur bei *Discocoelis tigrina*, sondern auch bei allen *Pseudoceriden* und *Eurylepta* nachweisen können. Ich glaube dass sie auch bei allen *Leptoplaniden* existirt, obschon sie hier schwer nachweisbar ist." Girard (1854) described the cleavage of *Planocera elliptica* as total and equal thruout. Later investigations on the polyclads have shown the cleavages to be unequal in those forms studied.

In *Leptoplana* the cells resulting from the second cleavage are also unequal in size, altho this inequality is not as marked as in *D. tigrina* and *P. inquilina*. This third cleavage results in two quartets of cells which are decidedly unequal in size, a condition similar to that in *D. tigrina*. In *P. inquilina* the difference in size, while sufficient to be easily recognized, is not as great as in *Leptoplana*.

There is a constant rhythm in the segmentation of the eggs of *Leptoplana*. In the second cleavage, the larger cell begins to divide in advance of the other. Lang found that in the case of *Discocoelis* the larger divides first, as: "Die Theilungerfolgt aber nicht ganz gleichzeitig, die grössere Furchungskugel theilt sich vielmehr etwas früher als die kleinere." In the third cleavage the larger cells also begin to divide in advance of the smaller. In the fourth cleavage it is a notable and constant fact that the macromeres split off a second quartet of micromeres before the first quartet completes its division. It is usually thought that in the case of unequal holoblastic segmentation that the presence of yolk material tends to retard division in the larger cells, so that the cells containing less yolk divide more rapidly, (this is the condition in the frog's egg) but in the case of the polyclads the presence of yolk material apparently does not retard cleavage. The cleavage of gasteropod eggs is like that of the polyclads in that the cells containing yolk divide in advance of the others.

CONCLUSIONS

The following conclusions regarding the maturation and segmentation of the living eggs of *Leptoplana* may be made:

1. The maturation divisions take place after the egg is deposited, and the second division follows closely after the first.
2. The cleavages of the egg are holoblastic and unequal.
3. The blastomeres do not divide synchronously.
4. The presence of yolk material in the cells does not retard cleavage since the larger cells divide in advance of the smaller.
5. The division is spiral and the cells rotate in dextrotropic or laetotropic directions.

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PLATE 1

LEPTOPLANA SP.

Fig. 1. Newly laid egg. *sh*, shell.

Fig. 2. First polar body. *1 p. b.*, first polar body; *sh*, shell.

Fig. 3. Egg at close of maturation division. *1 p. b.*, first polar body; *2 p. b.*, second polar body.

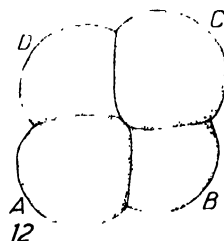
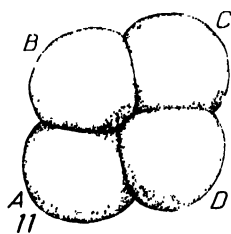
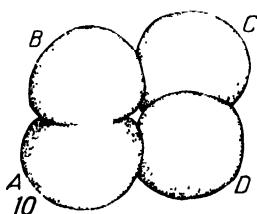
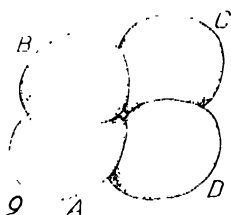
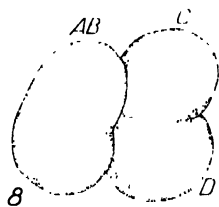
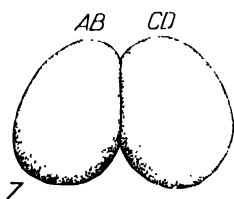
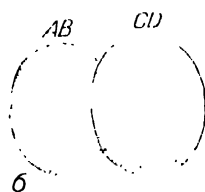
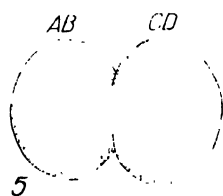
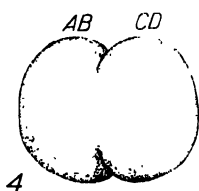
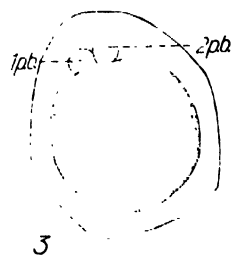
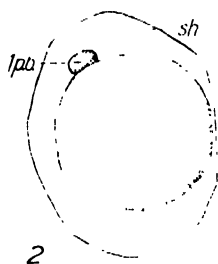
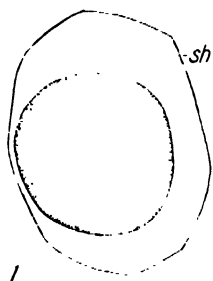
Figs. 4, 5 and 6. Stages in first cleavage. *AB*, smaller cell; *CD*, larger cell.

Fig. 7. Resting stage after first cleavage, showing flattening of blastomeres against each other. *AB*, smaller cell; *CD*, larger cell.

Figs. 8, 9 and 10. Stages in second cleavage. *CD*, divides in advance of *AB*.

Fig. 11. Resting stage at end of second cleavage, from animal pole. *B* and *D*, the smaller cells, in contact with each other at the animal pole.

Fig. 12. Same egg as in fig. 11, from vegetative pole. *A* and *C*, the larger cells, in contact with each other at the vegetative pole.



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Figs. 13, 14, 15, 16 and 17. Stages in third cleavage. *A*, *B*, *C* and *D*, macromeres; *1a*, *1b*, *1c* and *1d*, first quartet of micromeres.

Fig. 18. End of third cleavage. *A*, *B*, *C* and *D*, macromeres; *1a*, *1b*, *1c* and *1d*, first quartet of micromeres, shifting dextrorotically.

Fig. 19. Resting stage following third cleavage, lateral view. Labelling as in fig. 18.

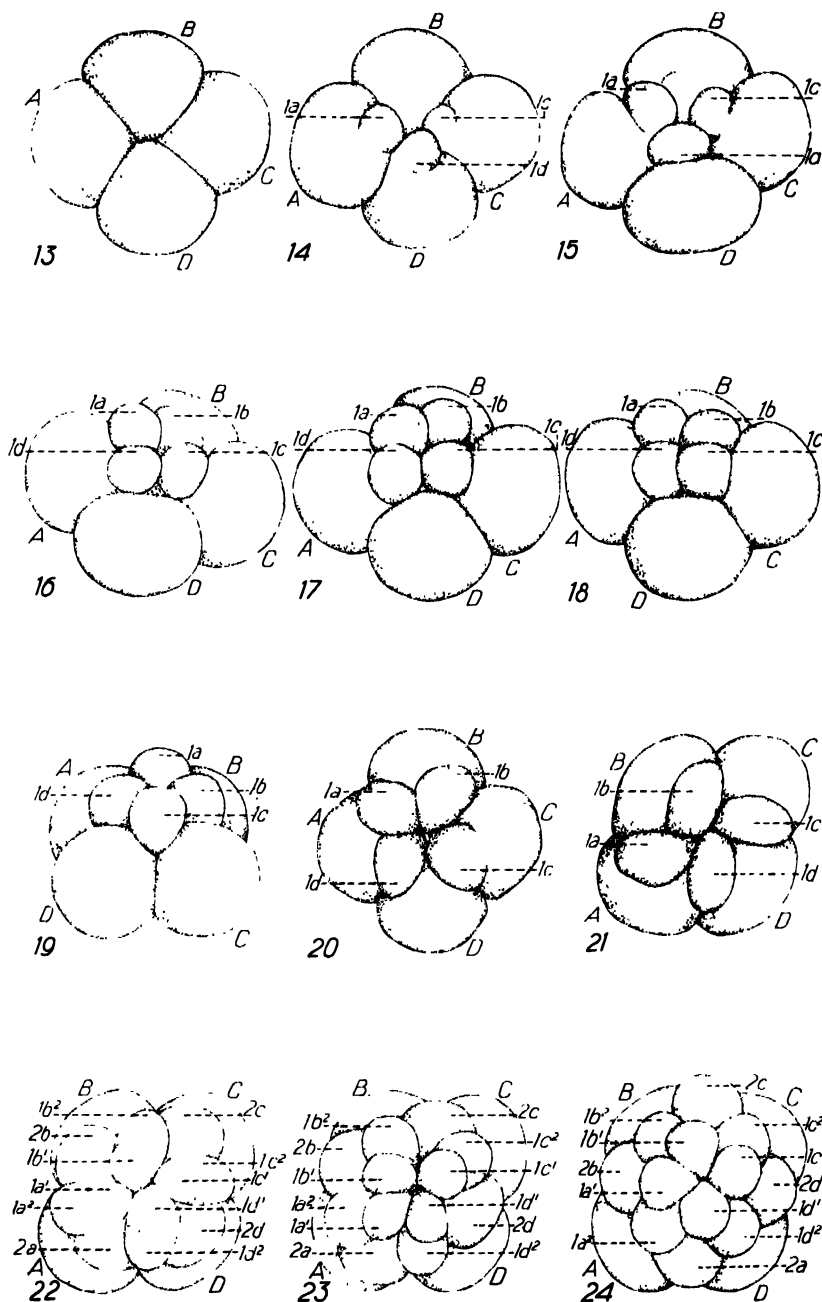
Fig. 20. Resting stage following third cleavage, from animal pole. Labelling as in fig. 18.

Fig. 21. Beginning of fourth cleavage. Elongation and shifting of *1a*, *1b*, *1c* and *1d*. Labelling as in fig. 18.

Fig. 22. Completion of second quartet of micromeres. *2a*, *2b*, *2c* and *2d* from *A*, *B*, *C* and *D*. Appearance of cleavage furrows in *1a*, *1b*, *1c* and *1d*. First quartet of micromeres. *A*, *B*, *C* and *D*, macromeres.

Fig. 23. Completion of division of *1a*, *1b*, *1c* and *1d*, first quartet of micromeres. Cells *1a*¹ and *1a*², from *1a*, *1b*¹ and *1b*² from *1b*, *1c*¹ and *1c*² from *1c*, and *1d*¹ and *1d*² from *1d*. First quartet of micromeres, *1a*¹, *1b*¹, *1c*¹ and *1d*¹, shifting dextrorotically; *1a*², *1b*², *1c*² and *1d*², micromeres separated from first quartet, shifting laeotropically; *2a*, *2b*, *2c* and *2d*, second quartet of micromeres, shifting laeotropically. *A*, *B*, *C* and *D*, macromeres.

Fig. 24. Resting stage at end of fourth cleavage, from animal pole. Labelling as in fig. 23.



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New Combinations in the Genus *Agoseris*

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In the revision of the difficult genus *Agoseris*, recognized also as *Troximon* by many taxonomists, a preliminary notice is hereby given of a few new combinations. A complete analysis of the genus with its respective species will be published in a later paper. The new combinations suggested are as follows:

1. *Agoseris glauca* var. *villosa* (Rydb.) new comb.

The variant includes all of the villose or pubescent forms of the *glauca* group. The leaves are either spatulate, lanceolate, or linear-lanceolate; the margins are entire, dentate, or slightly lacinate, and the plant as a whole is either dwarf, normal or fairly tall in size. All of these possibilities have been used as characters to define species. These poorly defined species have caused the existing confusion in the entire group. The type form is:

Montana: Helena 1891, F. D. Kelsey in the herbarium of the New York Bot. Gard.

2. *Agoseris grandiflora* var. *plebeia* (Gre.) new comb.

The *plebeia* form of Greene is merely a transition between *A. grandiflora* (Nutt.) Gre. and *A. laciniata* (Nutt.) Gre. When the terminal lobe of the leaves is broadly spatulate, the form is considered *A. grandiflora* (Nutt.) Gre. Should this same lobe be very linear and lacinate, the form is *A. laciniata* (Nutt.) Gre. It is natural to expect intermediate forms. These intermediates Greene recognized as *A. plebeia* Gre. The character is not sufficient to warrant the name of a species. Since this intermediate stage might confuse, the new combination is suggested. Type form: Baker No. 840 Santa Clara Co., Calif., in the U. S. Herb.

3. *Agoseris purpurea* var. *arizonica* (Gre.) new comb.

A form in the southwest, particularly in New Mexico, Arizona, Colorado, Nevada and Utah has retrorsely lobed or lacinate leaves similar to *A. glauca laciniata* (Eaton) Smiley with which it has been

confused. The form has the head of *A. purpurea* (Gray) Gre. The chief characters are: long achene with beak about again as long; short, blunt or rounded, ovate to nearly obovate outer bracts; both characters similar to *A. purpurea* (Gray) Gre. Leaves retrorsely laciniate or lobed. Plant sometimes dwarfed, appearing often very similar in habit to *A. apargioides* (Less.) Gre. when in the young state. The northern forms which have been confused with *A. gracilens* (Gray) Ktze. are taller and merge into *A. purpurea* (Gray) Gre. Type at the University of Notre Dame.

Delayed Germination in Seeds of *Peltandra virginica* and *Celastrus scandens*

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Received for publication April 10, 1928. —Editor

The popularity of native plants for use both in small gardens and on large estates in recent years has made the problem of delayed and restricted germination, so prevalent in the seeds of large numbers of the more attractive native shrubs and herbs, a matter of scientific interest from aesthetic reasons as well as scientific ones.

The causes of delayed germination in general have been well summarized by Crocker (1916), and may be briefly stated as follows: rudimentary embryos; inhibiting characters of seed coats, which result in mechanical resistance to embryonic expansion, prohibit gaseous exchange by the embryo and prevent water absorption; a combination of any or all of these factors; secondary dormancy due to unfavorable environmental conditions after the conclusion of an earlier dormant period.

The seeds studied were *Celastrus scandens* and *Peltandra virginica*. An attempt was made to study the microchemistry of the seeds and something of the physiological changes taking place in connection with the germinative tests made on them with the view of discovering how the structure and chemical content, and the changes occurring during after-ripening and germination, explained the lack of quick germinative power.

Unless otherwise stated seeds were prepared as follows for germination tests. They were washed in a 0.25% solution of uspulun to sterilize them, and placed on moist filter paper in sterile petri dishes. They were kept under varying conditions of light and temperature and watered when necessary with sterile tap water. On germination they were counted and removed to larger dishes, then later planted in the greenhouse.

Microchemical methods used were according to an outline furnished by Eckerson with the following exceptions for lipase activity and for acidity. The latter determinations were made with LaMotte apparatus, the former by testing the activity of a fat-free powder of

the seeds upon litmus milk under sterile conditions, the production of free acid being considered evidence of the activity of lipase.

PELTANDRA VIRGINICA

While considerable data is available as to the causes of delay in germination of various water plants, there has been no mention found, in the literature, of seeds of *Peltandra virginica* a plant growing rather commonly in the shallow mud-bottom edges of quiet streams in the eastern section of the United States. Muller (Crocker, 1916) found some years ago that seeds of *Eichhornia* do not germinate without desiccation. Fischer (1907) reported that acids and bases may hasten germination, and it was suggested and commonly held by the German botanists that the chemicals had a stimulating effect upon the protoplasm. Crocker (1907) and Crocker and Davis (1914) have succeeded, however, in establishing physico-chemical evidence for the known facts of germination of *Alisma*, *Sagittaria* and *Eichhornia* by finding that they germinated readily in distilled water, kept fresh, if the seed coat was broken or removed. Crocker and Davis (1914) report that in *Alisma*, at least, dormancy is due to the mechanical restraint of the seed coat, and that the effect of acids and bases seems to be in the weakening of the seed coats so that the imbibitional and osmotic swelling of the embryo is capable of breaking away the cap at the tip of the embryo. The acids and bases may also bring about a change in the water absorbing power of the pectic materials in the seeds.

Work on *Peltandra virginica* was confined to a study of the germination under varying conditions of light, moisture, temperature and season together with the microchemical and morphological examination.

Fruits when collected consist of clustered ovaries attached to a fleshy spadix. The seeds are enclosed within the dark rather leathery ovary wall, usually one in each ovary. It is this covering, not the seed coat, that proves the obstacle to germination. The ovary wall is thick and slippery on the inside. Outside there is a thin layer of cutin, while pectic materials are found in all other of its cell walls. There are numerous large air cavities in the wall. Besides pectic material the cell walls are of cellulose, no lignin being present. Pentoses, chloroplasts and some starch grains are present in the cells, with anthocyan in the cell sap of the epidermal layer. A mass of gelatinous pectic material encloses the seed which may average 6 mm in diameter. The cell walls of the papery seed coat are suberized

but this has a tendency to split readily; the suberin, therefore, can hardly inhibit water absorption. A thin layer of suberin also surrounds the endosperm, which tissue makes up the bulk of the seed. Its cells are packed with starch, a little chlorophyll and pentose sugar being present in the peripheral cells. The large well developed embryo of the monocot type lies at one side of the seed. It contains somewhat less starch than the endosperm tissue. In the hypocotyl region there are prominent groups of root initials which contain protein. Glucose sugar appears at the time of germination.

At all times the ovary wall proved susceptible to bacteria and fungi, while the pectic materials around the seed inhibited them. In all cases where germination occurred in seeds having intact ovary walls there was no germination until after bacterial and fungal growths had thoroly weakened the tissues of this pericarp. It was found that seeds with pericarp intact in stagnant water germinated after several weeks while those kept in fresh water had not done so.

SUMMARY

1. Seeds with the ovary wall intact do not germinate as long as kept free from molds and decay, but since it was impossible to keep them under completely sterile conditions indefinitely, decay eventually caused disintegration of the pericarp, thus permitting germination.

2. Germination of such seeds occurs more rapidly as the season advances, a fact that might be due to seasonal periodicity or to the attack of molds and bacteria on the pericarp during storage, making the deterioration more rapid after seeds are placed under germinating conditions.

3. When freed from the pericarp seeds germinate readily, over a period of several weeks, in light, at room temperature.

4. This germination exhibits seasonal periodicity, germination of 100% being secured in 47 days from seeds started in December, in 33 days if started in January and in 3 days when set up in March.

5. Germination occurs as readily in darkness as in light.

6. Refrigerator temperatures 5-10° C are as successful as room temperatures of about 20° C, seasonal periodicity being exhibited at these lower temperatures as well as at ordinary ones. In Seattle during February and March outdoor temperatures curtail germination but this does not operate thru curtailment of the rate of water absorption at the low temperature, since seeds thorly soaked before placing out of doors behave similarly.

7. Seeds with pericarp removed germinate more speedily if first soaked in water before placed under germinating conditions, tho the total per cent of germination and of time required is equal in either case, seeds not previously soaked germinating more rapidly after a first period of imbibition during which no germination occurs.

9. Seeds stored in water out of doors will begin germination with warmer spring weather, but in all cases a marked deterioration of the pericarp is noted to have taken place, in spite of all precautions to prevent it. Whether this is due to the unfavorable effect of lower outdoor temperatures upon germination or to the fact that, at higher or indoor temperatures, growth of molds and bacteria is favored, cannot be stated from the evidence thus far. Most probably both factors enter in.

10. The best germination, namely 100% in 3 days, was secured from seeds without ovary walls set up in the light at a temperature of 20° C on March 9th.

Dormancy in seeds of *Peltandra virginica* thus appears to be due largely to the inhibiting character of the ovary wall which prevents water absorption by the pectic materials about the seed. No germination occurred before a large amount of water had been thus absorbed. There is some tendency toward dormancy when seeds are first collected but this is steadily decreased with the advance of the season so that complete germination occurs immediately after absorption has been accomplished in the case of seeds placed under germinating conditions in March. The fact that the ovary wall is extremely subject to decay would suggest how it is possible for germination to occur in nature. Also the resistance of the seeds themselves to bacterial and fungal attack enables them to germinate readily after the disintegration of the pericarp.

CELASTRUS SCANDENS

At the time of undertaking this problem no data on the germination of *Celastrus scandens*, the Bittersweet vine native to the woods and hedgerows of the eastern section of the United States, could be found with the exception of that reported by Mitchell (1926). She reports failure of seeds to germinate within a period of six months when the seed coat remained intact. The removal or breaking of the seed coat brought about some germination, 9% in light at 20° C within 25 days, 23% in the dark at the same temperature, and 52% within 41 days at a temperature of 5-10° C.

Experiments conducted to check these results gave similar data altho the time required in all cases was somewhat longer. No

germination under any condition was secured when seed coats were intact, while the best germination, 66% during a period of 52-143 days, was secured from seeds with coats removed, in the dark, at 5-10° C.

This indicated that germination was inhibited by the seed coat but also that, regardless of the coat, a period of after-ripening was necessary. Attempts to cut short the dormant period by the use of stimulants such as ethylene chlorhydrin or butyric acid were unsuccessful. Freezing of the seeds was also ineffective.

A microchemical and morphological investigation disclosed the following points. The seed coat is composed of four distinct regions. A layer of cutin covers the seed. The inner walls of the epidermal cells contain pectic material. Below this lies a region of small flat irregular cells whose walls contain much pectin, and within which pentoses are found. Beneath these lies a layer of large squarish heavy-walled cells. In the walls is impregnated phlobaphane, an oxidation product of tannin, but the chief material is lignin. Below this and forming the inner layer of the coat is a layer of cellulose-walled cells. Fat droplets are scattered thru the coat.

The embryo and endosperm are composed of cells with walls of cellulose. The endosperm tissue is surrounded by a layer of suberin. Starch is absent from both endosperm and embryo but fat and protein are present in abundance. The endosperm contains phytosterol and lecithin, and pectic material in the region nearest the embryo. Lecithin and pectic material are also present in the embryo. Catalase activity was found to be low in dormant seeds, tho present; lipase activity was readily demonstrated. At the time of germination, beside the material already noted, amino acids and a reducing sugar, glucose, were found in the endosperm tissue, the former indicating hydrolysis of stored protein, and the latter, presumably, hydrolysis of stored fat thru the activity of the lipase with subsequent synthesis of sugar. Catalase activity was much greater than that found in fresh seeds and lipase was still active. Both starch and sugar were found in the hypocotyl when very young, and amino acids a little later, usually in the posterior region. Fat in the form of droplets was found in the root hairs, while the supply of fat and protein in the endosperm was distinctly diminished after germination.

Since there seemed no apparent lack of lipase activity in fresh seeds to account for failure to germinate promptly when seed coats were removed, other reasons were sought. Determination of acidity made with LaMotte's standard indicators gave the following pH values:

for the endosperm of fresh seeds 3 months after collection, 8.8; after 8 months storage, 8.0; and for the same lot of seeds just germinated, 7.4. The embryo of seeds 3 months after collection shows a pH of 8.8, while the pH after 8 months storage was 7.8, and after germination 7.2. Thus there is a steady increase in acidity both during a period of storage and thru a period of after-ripening under germinating conditions.

In order to determine what part water absorption might play in germination, seeds with and without coats were soaked for varying periods and then placed under germinating conditions. Seeds with coats on absorbed 51.9% of their weight in 273 hours. When the coats were then removed, calculating from a known average weight of the same number of coatless seeds, they were found to have absorbed 28% of their weight thru the coats; that is, the endosperm and embryo had absorbed that per cent of the total original weight. Seeds without coats in 107 hours absorbed 37.2% of their weight. Absorption ceased at this point in the case of coatless seeds. This indicates, therefore, that the structure of the seed coat is not such as to inhibit germination from lack of water absorption since considerable absorption takes place thru the coats.

Thus dormancy in seeds of *Celastrus scandens* depends upon two factors: the mechanical restraint of the seed coat which inhibits growth; and the requirement of the seed for an after-ripening period during which there is a gradual increase in acidity of the embryo and endosperm, and of catalase activity. Within a period of 179 days, no germination was secured from seeds with coats intact. The limitations imposed by the academic year, however, precluded obtaining any evidence for the effect of a longer time interval. The best germination of coatless seeds was secured by germinating them in the dark at a temperature of 5-10° C. During a period of 52-143 days a germination of 66% was obtained.

Acknowledgements are due Dr. E. A. Roberts for suggesting the problems and for criticisms during the first year at Vassar College; to Dr. S. H. Eckerson for directions for the microchemical work; and to Dr. G. B. Rigg for criticisms and direction during the second year of the investigation at the University of Washington.

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Observations on the Spawning Habits of *Melibe Leonina* (Gould)

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The nudibranchiate mollusc *Melibe leonina* (Gould) has been used rather extensively whenever available as a source of material for the course in embryology at the Puget Sound Biological Station, at Friday Harbor, Washington. These animals are commonly found on eelgrass (*Zostera marina*) and occasionally on other marine plants in the vicinity of the Station. The egg masses, or nidosomes, occur on the eelgrass as broad spiral ribbons, 3 to 4 cm in breadth and 7 to 10 cm in length. A large bed of eelgrass, a favorite habitat, along the edge of Brown Island, near the laboratory, furnishes an ideal location for observations on the spawning habits of *Melibe leonina*. In this area the writer has made more or less detailed observations on this species of mollusc during the summers of 1924, 1925, 1926, 1927, and 1928.

The systematic relationships and detailed morphology of *Melibe leonina* have been established and very definitely worked out in two publications by Agersborg (1919 and 1923). His studies cover nearly every point in regard to the morphology and histology of this species, including a very comprehensive review of the literature with an excellent bibliography.

The studies undertaken here are only the spawning habits of this species of mollusc because certain peculiarities were noted which created so much interest that it seemed worthy of record. A striking difference in the the number of individuals from year to year is very evident from the present study. In the summer of 1924 *Melibe* was fairly abundant and egg masses could be found at almost any time from June 15 to about July 10. They were extremely scarce in 1925; in fact, not a single specimen was found altho a very thoro search was made for them from June 15 to July 20. Thruout the same period only a very few egg masses could be obtained. The summer of 1926 found *Melibe* more abundant and the animals were frequently observed on the eelgrass, and the egg masses were plentiful. In 1927 there appeared to be a decrease in number from the previous year,

and only an occasional specimen could be found in the eelgrass. Some egg masses were obtained but they were relatively scarce. During the present summer (1928), these animals were found on the eelgrass in very large numbers during the latter part of June and the early part of July. Egg masses literally covered the eelgrass in certain of the areas under observation. From the foregoing survey one readily notes the peculiar variation in the number of animals from season to season. Such spasmodic fluctuations in numbers from year to year have been witnessed by Agersborg (1919:270).

The spawning period of *Melibe leonina* has been observed by Bovard and Osterud (1918:134) who state that it occurs early rather than late in the summer but give no dates. Ordinarily, it spawns in June and July but Agersborg (1919:270) states that it has been seen spawning in March. This, no doubt, is an unusual occurrence and should not be normally expected. In the present study it has been observed that apparently, very little spawning takes place before June 20. The writer has been somewhat handicapped by the fact that he has been unable to make any observations on the spawning habits of this nudibranch before June 15 during the five seasons over which the study has extended. On only one occasion in the present work were eggs found before June 20 and that was during the season of 1926 when a single freshly deposited mass was obtained on June 18. During the present season (1928) the first egg mass was obtained on June 23. These eggs had probably been deposited on the preceding day as they were undergoing development and had advanced to about the 24 to 28 hour stage. From the above we glean that the beginning of the spawning period is ordinarily about June 20. However, there may be occasional egg masses deposited earlier in the year but it appears from our experience that such an occurrence would be an exceptional rather than a normal condition.

The duration of the spawning period is also a matter of some interest. This has not been noted as closely as has been the beginning of the period. The marked fluctuations in number from year to year have made it difficult to determine the period when the height of spawning is reached. For instance, during the season of 1925 not a single animal was seen and very few egg masses could be obtained. However, in seasons when these nudibranchs are more abundant we find that the greatest fecundity occurs between the first and tenth of July. Egg production continues ordinarily until about August 1. Occasionally, there may be an isolated egg mass seen on the eelgrass after this date but such is unusual.

Particularly careful observations were made on the spawning habits of *Melibe* in the summer of 1928. Records were taken almost every day from June 20 until August 15. The location taken for study was an area of eelgrass, south of Brown Island, about 300 yards long and from 6 to 15 yards wide. In the other years the same location was used for observation but the entire area was not covered as thoroly. At extreme low tide a small portion of this plot was exposed. The area was covered almost daily by paddling about in a small boat and making the observations from it. Careful records were made of the number of animals seen, the number mating and the approximate number of egg masses. Climatic conditions were also noted as it was apparent that such factors might influence the presence of the animals.

The first observations for the season 1928 were made on June 17 and on that date no animals or egg masses were seen. The first egg mass was obtained on June 23 and on this date the first molluscs were recorded when three animals were seen on the eelgrass at 10 o'clock, A.M. On this date the weather was clear but the water was rough. Following this date a few new egg masses were observed each day but no more animals were recorded until June 29, at 9:30 A.M., when some were found. Between the 23rd and 29th of June the weather was generally cloudy and windy, with rough water, which might have affected the presence of the animals. On June 29 the weather was clear but the water was rough. One pair of *Melibe* was taken in copulation and after an extensive search 25 specimens were recorded. A slight increase in the number of egg masses was noted. On June 30 almost a hundred of the nudibranchs were counted on the eelgrass and these were nearly all high up on the vegetation. Five pairs were found in copulation. A further increase in the number of egg masses was observed. The weather was cloudy and the water was perfectly smooth. Twenty-five specimens were collected and placed with some eelgrass in a live box on the Station float.

The greatest number of specimens of *Melibe leonina* were observed on July 1 when perhaps 1000 individuals appeared on the eelgrass in the particular area used in this investigation. At least 150 pairs were found in copulation. Upon examination it was found that some were in single mating but the majority were in mutual coitus. Agersborg (1919:570) states that mutual coitus has not been observed in *Melibe*. During the act of copulation the animals lie side by side, or with the bottom of the foot of each together, with their heads in

opposite directions, and the penis of each is inserted into the vaginal pore of the other. The penis is a long screw-like organ about 25 mm in length and of tough fibrous material. When the act of coitus is effected the two animals are so firmly attached that they can be handled rather roughly without becoming separated. Twenty-five mating pairs were collected with a dip net from their habitat on the eelgrass and placed in a bucket by means of which they were transported to the live-boxes. The union during copulation was so firmly established that when the animals were released in the boxes the majority of the pairs were still attached. On this date the sky was clouded over and the water was smooth. A marked increase in the number of egg masses was recorded.

The next day, July 2, the sky was clouded over and the water was particularly smooth when observations were made at 9:00 o'clock. Only 30 animals were found on the eelgrass and these were mostly low down on the vegetation. Four pairs were found in the act of copulation, all in mutual coitus. Several individuals were observed in the act of depositing egg masses. A very marked increase in the number of egg masses was noted. Upon returning to the float an examination of the animals in the live box revealed one pair in single mating. In the afternoon of the same day another pair was found in mutual coitus. Several egg masses were deposited in the live box.

Observations were made at 8:00 o'clock, A.M. on July 3. The weather was rainy and the water was rough. Eight specimens were seen on the eelgrass and these were all low down in the water. There were none seen in the act of mating. The increase in the egg production was enormous; in fact, the eelgrass was literally covered with egg masses in certain sections of the area inhabited by *Melibe*. Two pairs were mating in the live box and several new egg masses had been produced.

Ten specimens were counted on July 4 when the eelgrass area was visited. These were low down on the vegetation and none were in the act of mating. There was a large increase in the number of egg masses over that of the previous day. The sky was cloudy and the water was quite rough. No matings were observed in the live box but there was an increased egg production by the animals in captivity. Two of the animals were examined while in the act of depositing eggs. A survey of the eel-grass area was made at 10 o'clock on July 5. Thirty-seven *Melibe* were seen well down on the vegetation and of these six pairs were in the act of copulation. There was

a continued increase in egg production. By this time the eelgrass held so many egg masses in various stages of development that it really presented a unique spectacle. On this date the sky was clear and the water was smooth. The animals held in the live boxes continued to deposit eggs but none were observed mating.

Observations after this date indicated that the height of the spawning season had been reached and that the egg production began to decline. On July 6 only four of the nudibranchs were found in the field and these were low on the eelgrass. There was an apparent decrease in the egg production. In the live boxes there were no matings and no eggs produced. This was carefully noted and checked because each day the egg masses were removed from the eelgrass with the captive animals. Six specimens were noted in the field on July 7 and egg production was near its height. One pair was found mating in captivity and five egg masses were produced by the 50 captive animals.

On July 8 four animals were seen in the field and none could be found again on the eelgrass until July 12, when one living specimen and two dead ones were found. During this time there was a particularly noticeable decrease in new egg masses from day to day. In the live boxes there was an occasional mating observed and egg production continued until July 16. On July 11 several of the animals were noticed to be shrinking in size and two were dead. This could not have resulted from lack of food because there was an abundance of plankton on the eelgrass upon which these nudibranchs were living. This condition of the shrinkage in size of some of the animals in the live box continued even tho egg masses were produced for some days after its onset. The nudibranchs in captivity began dying on July 13. The last mating among the captive animals was on July 15. Each day it was noted that more of the captive nudibranchs were becoming shrunken in size and that the death rate increased until July 23 when the last of the 50 captive animals died. Field observations indicated a somewhat similar but perhaps not so marked a condition. On July 14 three living animals and one dead one were recorded. The dead animals showed the same shrunken appearance as that presented by the captive animals. Very few new egg masses were found in the field. Field observations, continued daily, showed a decreasing egg production and none of the molluscs could be found on the eelgrass until July 20 when three living and one dead animal were found. The dead *Melibe* presented the same shriveled appearance as shown by those in captivity. Visits to the

field revealed no more of the nudibranchs until July 29 when one dead animal, much shrunken, was found floating on the surface. Six freshly laid egg masses were seen on the eelgrass on this date. On July 30 two dead animals were observed on the *Ulva* near Brown Island. An apparently young *Melibe*, about 25 mm in length, was taken on the eelgrass on July 31.

The last freshly deposited egg masses for the season 1928 were observed on August 7, and the last animal recorded on the eelgrass for this season was on August 12.

From the foregoing we note that *Melibe leonina* shows spasmodic fluctuations in numbers from year to year. This has been observed by other workers who have been at the Station in former years. It is a baffling problem to determine the reason for such variations. A similar phenomenon has been observed by the writer in regard to some other animals in the immediate vicinity of the Station. Perhaps, in the case of *Melibe*, it may be that the scarcity is more apparent than real from the fact that the animals can readily be observed in large numbers only for a short period during the height of the spawning season.

Light and weather conditions undoubtedly influence the number of the nudibranchs that may be seen on the vegetation in the area under observation. It was rather apparent that directly preceding and immediately following the height of the spawning season weather conditions did materially affect the number of animals present. On days when the sky was clear and the water rough very few animals were visible on the eelgrass. During cloudy weather more animals could ordinarily be seen than on clear days. More of the nudibranchs made their appearance when the water was smooth than when rough; in fact, that appeared to be a greater influence than the light factor. When the spawning period was at its height neither light nor the roughness of the water had any apparent effect upon the presence of the animals. They were visible in large numbers at all hours of the day regardless of the light and wind factors. However, most of the eggs are deposited during the night or early in the morning, and consequently one can only surmise in regard to the factor of illumination.

One of the most peculiar and interesting phenomena observed in connection with the work was the accumulation of enormous numbers of animals on the eelgrass during the short period from June 29 to July 3, 1928. During this period the nudibranchs were not only attached to the eelgrass but many were floating or swimming

about. Associated with the swarming of *Melibe* there were observed many pairs in the act of copulation. This was of peculiar interest as it was discovered upon examination that the majority of the mating animals were in mutual coitus, a relationship heretofore unobserved for this nudibranch.

Fifty of the molluscs were confined in live boxes and observed daily. These mated and produced many egg masses after which they became shrunken in size and finally died. This is of particular interest on account of the fact that a similar condition was observed to some extent in the field. A number of dead nudibranchs were found there immediately after the height of spawning but undoubtedly the percentage was small because the dead animals settled to the bottom and could not readily be distinguished beneath the vegetation. This seems to indicate that unquestionably many, if not all of the *Melibe*, die shortly after they have spawned. Naturally this would bring up some questions in regard to the length of life of this mollusc. Does it live for only one year or does it have a longer span of life? Does *Melibe* spawn more than once during its lifetime? The observations made here seem to indicate that the animal spawns once and that it lives for only one year. No animals apparently immature have been found at any time preceding the spawning season or while fecundity is at its height. On several occasions during the five seasons over which this study was continued, small *Melibes*, up to 25 mm in length, have been obtained during the early part of August. These were considered to be young individuals which had been reared during the season in which they were found and not from the preceding one. This is a problem which needs grater elucidation thru a detailed study of the life history of nudibranchs in general.

The problem of spasmodic variations in numbers of nudibranchs, as well as of other animals, is an interesting one and needs to be investigated in order that the cause may be determined. Whether it is simply a matter of number of individuals or whether it is due to their migratory habits should be ascertained. Phenomena associated with spawning habits of nudibranchs are only slightly known and therefore many investigations are needed to clear up the various phases of these interesting problems.

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The Behavior of Sea Water, Lake Water and Bog Water at Different Carbon Dioxide Tensions

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INTRODUCTION

In the early part of last year a field method for the colorimetric determination of the carbon dioxide tensions of natural waters was worked out (Powers, 1927). This method was the outcome of the author's application of our present knowledge of the behavior of carbon dioxide in solution to data obtained by subjecting in the laboratory eleven different samples of natural waters to various carbon dioxide partial pressures of the atmosphere between about 0.3, that is, the carbon dioxide partial pressure of the air, and about 50 mm of Hg. When a mathematical analysis of theory and data was made (Powers and Bond, 1927), it was found that there was more or less of a linear relation between the pH and the logarithm of some constant factor of the carbon dioxide tension of the water. The linear relation, expected according to the theory, held very closely in water samples numbers 6, 7 and 8. The error in the ratio between the two sides of the equation, $\text{pH} = -n \log(Kk_{\text{gas}}P)$, was in the second or third decimal place, when given values were substituted for K and k_{gas} and the determined value substituted for n . It was found that errors were greater and in opposite directions in waters more alkaline or more acid than the three samples of water, that is, numbers 6, 7 and 8. The greater the alkalinity or acidity the greater was the error. In the most acid water, number 2, the error was practically in the first decimal place at the extreme carbon dioxide tensions.

The attention of the authors, Powers and Bond (1927), was called to the fact that they had expressed the carbon dioxide tension of the water in mm of Hg instead of per cent of an atmosphere. The solubility factor of carbon dioxide in water, k_{gas} , is expressed in molar terms and P, the carbon dioxide tension of the water, in per cent of an atmosphere. The author, in recalculating data given in table 1 on pages 473-475 of Powers and Bond (1927), found that when the carbon dioxide tensions were expressed in per cent of an atmosphere the errors were least in water samples numbers 4 and 5.

The errors increased with increase in alkalinity and with increase in acidity and as before in opposite directions.

When the data of Powers and Bond were examined more carefully it was found to be obvious that there was an error in the assumed value of K or K_{gas} or Kk_{gas} and that this error was characteristic of each natural water. To correct for this error the correcting factor has been introduced into the equation which now becomes $\text{pH} = -n(\log P + e)$ (Powers and Bond, 1928). When this formula is applied the error in the ratio of the two sides of the equation is in the second, in reality in the third, decimal place and is in no way associated with the alkalinity or acidity of the water.

Since this method was tried on various stream waters and a spring water, it was thought advisable to test it on sea water, lake waters of different types and bog water. The last represents water with an extreme organic content and the first with an extreme inorganic content.

MATERIALS

The waters selected for these observations were sea water, collected the morning of July 17 in the open water near the Puget Sound Biological Station; waters from the Upper Lake, about 374 feet elevation, and Lower Lake, about 188 feet elevation, on Blakely Island, collected July 9; water from Sportsmans Lake, on San Juan Island, collected July 17; and open bog water and bog water collected July 8 from a bog about 275 feet elevation on Blakely Island near Thatcher Post Office. The bog water was collected from water drained into a hole dug $3\frac{1}{2}$ feet below the surface, and the open bog water was taken from open water at the lower end of this same bog. All samples of water were stored in clean Pyrex glass flasks and tightly stoppered with cork stoppers.

METHODS

All water samples, with the exception of the sea water, bog water, and open bog water, were divided into two equal portions. One portion of each was kept in the open in direct sunlight and the other portion of each was kept in a dark room for about 25 to 40 days. The bog water was divided into three portions. Two of the three portions were treated in the same way as the above samples. A third portion of the bog water was aerated, for the last 25 days preceding the testing of all water samples, by drawing air thru it very slowly by means of a filter pump. The air was first drawn

thru distilled water to prevent evaporation of the water sample. The volume of this water sample had not changed during the 25 days of aeration, so far as could be estimated in a 500 cc Erlenmeyer Pyrex glass flask. The volume of the water was not actually measured before or after the aeration. This was a precaution against possible contamination thru handling. The aeration was carried on in the laboratory in ordinary light. The sea water sample was stored in a 6,000 cc Pyrex glass flask. The open bog water was stored in the dark room. An accident had befallen the sample of bog water which was to have been placed in the sunlight.

The testing of these samples of water continued over a period of 7 days, August 11 to 17. Two or three cc of each of the samples of water to which an indicator had been added were aerated with air of a known carbon dioxide partial pressure from a five gallon bottle. The air was forced out of the five gallon bottle by forcing water, protected by a covering of paraffin oil, into the bottle by means of a long glass tube extending to the bottom of the bottle. The air was first forced thru distilled water, and then thru a small Pyrex glass tube, and allowed to escape at the bottom of the Pyrex glass test-tube containing the two or three cc of water sample to be tested. This manipulation prevented evaporation of the water sample during prolonged aeration. After aeration, the water sample was compared with LaMotte color standards, having 0.1 pH intervals. The pH was estimated to the 0.01 place.

Pyrex glass only was allowed to come in contact with either water samples or indicator solutions. The indicator solutions used with sea water were made in the same sea water to be tested. All other indicator solutions were made up in distilled water. Errors due to the addition of indicators might have been avoided, had each indicator solution been made up in the water to be tested, since there was always a dilution of the water sample to be tested by addition of the indicator and the dilution was not proportionate in the different water samples since different indicators were unequally soluble in the distilled water. Saturated solutions of indicators were used. All tests were made at 15° C, this being a convenient and easily controlled temperature of a water bath composed of a three gallon galvanized bucket.

The barometric reading was taken for each test and the carbon dioxide partial pressure was reduced to per cent of an atmosphere.

EXPERIMENTAL DATA

Table 1 shows the ratio between the pH and the value of $-n(\log P + e)$ in the equation $\text{pH} = -n(\log P + e)$ of the various waters tested at different carbon dioxide tensions.

The equation $\text{pH} = -n(\log P + e)$ is the mathematical expression of the relation between pH and the carbon dioxide tension of a given sample of water and is known as the Power Law.

pH is the acidity or alkalinity of the water sample, e is the $\log(Kk_{\text{gas}})$ and is characteristic for each water sample. K is taken to be 3.40×10^{-7} (Johnston, 1915). k_{gas} , the solubility factor of carbon dioxide in water (Stieglitz, 1909), is calculated from the equation $e = \log(Kk_{\text{gas}})$. Since e is not a constant k_{gas} is not a constant but is characteristic for each water sample.* P is the carbon dioxide tension of the water expressed in per cent of an atmosphere. n is the rate of change of pH per unit change in $-(\log P + e)$ and varies with each water sample.

Just how nearly the ratio between the pH and the calculated value of $-n(\log P + e)$ of the different water samples is equal to unity is shown in columns three and six of table 1. The error is in the second decimal place and for the most part is in the third decimal place.

In Upper and Lower lake and open bog waters the determined values of e or n or both are in error. In the first two the ratios are 1.000 and below, and in the open bog water the ratios are 1.006 and above.

The sources of error are errors in reading the pH of the water, in measuring the carbon dioxide partial pressure of the atmosphere with which the carbon dioxide tension of the water has been brought into equilibrium, and in the incompleteness with which this equilibrium has been attained. The greatest error is in reading the pH

*There are reasons why e should not be reduced to terms of $\log Kk_{\text{gas}}$, that is to terms of k_{gas} . First, the equation contains the factor K , the ionization constant of H_2CO_3 into H^+ and HCO_3^- which is calculated on a false premise, that is, the assumption that all the CO_2 in solution is in the form of H_2CO_3 and the ionized products of H_2CO_3 , and that none exists in the form of CO_2 . Second when it is recognized that the CO_2 exists in solution as CO_2 , H_2CO_3 , HCO_3^- and CO_3^{--} the relative ratios between these are not known. Third, it is not known whether or not the ratio between CO_2 and H_2CO_3 is a constant or whether or not it varies with the acid and alkali reserves of the solution. Fourth, the concentrations of HCO_3^- and CO_3^{--} are determined by the CO_2 tension of the solution alone only when the acid and alkali reserves are zero. In other words, the acid reserve decreases the HCO_3^- and CO_3^{--} , and the alkali reserve (bicarbonates and carbonates) increases the HCO_3^- and CO_3^{--} in solution.

These points need further elucidation. Until they are cleared thru data obtained from experimental observation we will reduce the factor e to terms of $\log Kk_{\text{gas}}$.

TABLE 1. The ratios between the pH and $-n(\log P + e)$ in the equation $\text{pH} = -n(\log P + e)$ and the values of n and k_{gas} are given for the different water samples tested at 15° C at various carbon dioxide tensions.

pH of water	CO ₂ partial pressure in per cent of an atmosphere	$\frac{n(\log P + e)}{\text{pH}}$	pH of water	CO ₂ partial pressure in per cent of an atmosphere	$\frac{n(\log P + e)}{\text{pH}}$
Sea water		$n = .9696$ $k_{\text{gas}} = 22.21$	Open bog water		$n = .9679$ $k_{\text{gas}} = 67.$
8.30	.028+	1.010	7.84	.028+	1.010
7.23	0.55+	.995	6.57	0.55+	1.017
6.83	1.30+	.997	6.18	1.30+	1.022
6.52	2.62+	1.000	5.93	2.62+	1.018
6.36	3.88+	1.002	5.72	3.88+	1.006
6.23	4.04+	.997	5.62	4.04+	1.016
Upper Lake water		$n = .9333$ $k_{\text{gas}} = 16.64$	Lower Lake water		$n = .9333$ $k_{\text{gas}} = 16.64$
7.87	.028+	1.000	7.87	.028+	1.000
6.73	0.55+	.998	6.73	0.55+	.998
6.36	1.30 +	1.000	6.37	1.30 +	1.000
6.14	2.62+	.992	6.13	2.62+	.992
5.93	3.88+	1.000	5.93	3.88+	1.000
5.83	4.04+	.997	5.83	4.04+	.997
Sportsman's Lake water (kept in light)		$n = .8616$ $k_{\text{gas}} = 12.80$	Sportsman's Lake water (kept in dark)		$n = .8614$ $k_{\text{gas}} = 12.80$
7.69	.028+	.999	7.67	.028+	1.000
6.58	0.55+	1.001	6.57	0.55+	1.001
6.23	1.30+	1.001	6.20	1.30+	1.006
6.00	2.62+	.994	5.97	2.62+	1.001
5.84	3.88+	.999	5.82	3.88+	1.002
5.72	4.04+	.996	5.70	4.04+	1.000
Bog water (kept in light)		$n = .05748$ $k_{\text{gas}} = 2.87 \times 10^{-63}$	Bog water (kept in dark)		$n = .05748$ $k_{\text{gas}} = 2.87 \times 10^{-63}$
4.20	.028+		4.07	.028+	
4.19	0.55+		4.07	0.55+	
4.23	1.30+		4.04	1.30+	
4.21	2.62+		4.08	2.62+	
4.13	3.88+		4.06	3.88+	
4.07	4.04+		4.03	4.04+	
Bog water; portion aerated for about twenty-five days;					
		$n = .05748,$ $k_{\text{gas}} = 2.87 \times 10^{-63}$			
4.17	.028+	1.000	4.10	2.62+	.989
4.16	0.55+	.990	4.07	3.88+	.995
4.15	1.30+	.980	4.04	4.04+	1.000

of the water which is in the second decimal place. pH values are negative logarithms. Thus the error from this source is the error in using two-place logarithms with an error in the second decimal place. The extent of this and other errors are dependent upon technique.

Due to the form of the equation, $\text{pH} = -n(\log P + e)$, the errors in e and n tend to compensate each other. There is a tendency for values for e to be low when n is low. These observations show no absolute coordination in this respect. The number of different waters tested is too small to enable one to reach any definite conclusions on this point.

No corrections have been made in the pH readings for salt error for sea water or any of the other waters. In an error of 0.2 pH units in extreme readings of 8.00 to 4.00 pH the error in the value of n would be less than 3% of the actual value of n . This is less than the experimental error of the method.

SUMMARY

In all water samples the pH values show a linear relation to the values of $-(\log P + e)$, that is $\frac{-n(\log P + e)}{\text{pH}} = 1.00 \pm$, in the equation $\text{pH} = -n(\log P + e)$, at different carbon dioxide tensions with only slight errors which are within the experimental error of the method.

There were no detectable differences in the pH values at any given carbon dioxide tension between either Upper or Lower Lake water that had been stored in the direct sunlight and that stored in a dark room for some 25 to 40 days. The waters of Sportsmans Lake, unlike the waters from Upper and Lower Lakes, showed a detectable difference in pH values at a given carbon dioxide tension after storage in direct sunlight, and after storage in a dark room for from 25 to 40 days. The water that had been kept in the direct sunlight always had a higher pH at any given carbon dioxide tension than the water that had been kept in the dark room (see table 2).

The only sample of water from the open bog was stored in a dark room from 35 to 40 days before tests were made. Thus the effect of sunlight was not determined. There was a decrease in the alkali reserve of the open bog water on standing as shown by the lower pH on aeration (see table 2). This change could have been due to some weaker organic acid oxidizing to form a stronger acid. Or a more probable explanation might be that this change was brought about by the formation of hydrogen sulphide which was oxidized to sul-

TABLE 2. *Showing the increase or decrease in pH after ageing of air equilibrated water at 15° C.*

Kind of water	When collected	Stored in dark room for about 35 days	Aerated for 25 days	Stored in direct sunlight for about 35 days
Open bog water.....	7.89	7.84		
Sportsman's lake water	7.62	7.67		7.69
Bog water.....	3.98	4.07	4.17	4.20

phuric acid which in turn neutralized bases present in the water in the form of carbonates and bicarbonates.

The bog water, when collected, was divided into three portions. One portion was placed in direct sunlight, another in a dark room, and the last portion was aerated for about 25 days as has already been described. By an inspection of tables 1 and 2 it is seen that the pH values of the portion of the water sample kept in the dark room were always the lowest of the three portions and of that kept in direct sunlight, the highest; the pH values of that which was aerated were always between the other two at any given carbon dioxide tension. The portion which was aerated for the 25 day period showed a very little greater error in the ratio between the pH and the $-n(\log P + e)$ values than that of other waters tested. The pH values in relation to the $-n(\log P + e)$ in the other two portions are more or less irregular and have not been calculated.

It is the opinion of the author that the three portions of the bog water sample were undergoing a gradual chemical change and thus this chemical change in the species in solution had not proceeded equally in all parts of a portion of the water sample, and that when samples were drawn off to test they were not uniform except in the portion that had been aerated, that is, thoroly mixed. Shaking of the portions that were kept in the sunlight and in the dark room was purposely avoided to prevent stirring up sediment which had settled out.

DISCUSSION

From the foregoing experiments it seems that the carbon dioxide tension of natural waters can be determined by the method described by Powers (1927) and Powers and Bond (1927 and 1928). Organic and inorganic matter seemingly do not interfere. In order to obtain

absolute, and not relative values for the carbon dioxide tension of natural waters, the actual partial carbon dioxide pressure of the air used for aeration must be known. This can be determined colorimetrically as described by Higgins and Marriott (1927) and by Powers (1927). More accurate values for the carbon dioxide tensions of natural waters can be obtained by aerating with air having a known carbon dioxide per cent composition from a container. Still more accurate results can be obtained by the use of quinhydrone electrode. In the field, readings of the pH must be taken at two known carbon dioxide tensions. The greater the difference between the two known carbon dioxide tensions the more accurate the results, since the errors in reading the pH values become relatively smaller. It is fortunate that the carbon dioxide partial pressure of the alveolar air is about 200 times that of the air. Bog water and water presumably containing organic matter in solution behave differently from that of ordinary water when stored either in or out of direct sunlight. The only other work that the author knows which attempts to test the effect of sunlight on the behavior of water is that of Powers (unpublished) on mountain streams. This point is discussed in more detail in that article. Suffice it to state here that the actual alkali reserves of waters from Sportsmans Lake and from the bog on Blakely Island were increased by ageing in the dark but more rapidly in the direct sunlight as is shown by the increase in the pH values of these waters aerated under experimental conditions (see table 2). The open bog water underwent a change by ageing in the dark but in the opposite direction from that of bog water. The changes brought about in the waters of Sportsmans Lake, the open bog and the bog, could not have been due to blowing out of a volatile acid in the one case stronger than carbonic acid and in the other case weaker than carbonic acid, since the readings in each case were taken at 15° C after vigorous aeration of each sample of water, and would have been the same in each of the three samples. Furthermore, the portion of bog water aerated for the 25 day period did not show as high an alkali reserve as did the portion that was kept in the direct sunlight. The behavior of the water seemed to be due to one or the other or both of two possible changes taking place in the water. First, this might be due to slow oxidation of organic acids which takes place more rapidly in direct sunlight. Second, this might be due to bacterial action (Birge and Juday, 1922, and Greenfield and Edler, 1926), again the action being more vigorous in sunlight than in darkness. Evidences that there is an oxidation, thru

bacterial action or otherwise which progresses more rapidly in sunlight are given by Powers (unpublished).

Thompson, Lorah and Rigg (1927) have called attention to the fact that the acidity of bog water from two bogs, Esperance and Ronald, were increased when the carbon dioxide was removed. It was suggested by these authors that this might be due to the buffering effect of the weaker acid, carbonic, or the stronger acid, the organic acid in solution. Another probable explanation is that carbon dioxide is loosely held in combination by the organic material or organic acids which in the one case forms an acid less strongly ionizable than the original acid, and in the second case more strongly ionizable. This is not an entirely new conception. Noyes and Yonder (1918) state: "The work of Coville and others has shown that organic matter is acid in reaction at certain stages of its decay. We are aware of no work that absolutely proves that this acidity is other than that due to carbonic acid weakly held by the organic matter." If such a combination is formed the reaction is very slow and is seemingly not speeded up by an increase in carbon dioxide tension.

When table 1 is examined in more detail it is found that there are great variations in the values of n and of e in different natural waters. n , which indicates the rate of change in pH with the change in the logarithm of some factor of the carbon dioxide tension of the water, seems to be an index of the alkali reserve of the water. Thus a water with a value of .5000 for n would be pure water or water containing only neutral salts in solution. Such a statement was made by Powers and Bond (1927). This, however, needs further verification in view of the great variations in e , that is, the $\log(Kk_{\text{gas}})$, in reality the product Kk_{gas} .

The great variation in the product, Kk_{gas} , presumably k_{gas} since K is supposed to remain constant for any one temperature, is one of the unexpected findings of this investigation. Data recorded in this paper and by Powers and Bond (1927), recalculated, show very plainly that the k_{gas} , the solubility factor of carbon dioxide in water, decreases with acidity and increases with alkalinity. On second thought the behavior of k_{gas} as found in this investigation is the expected rather than the unexpected. It is common practice in all freshman chemical laboratories to force carbon dioxide out of solution in all types of water, including distilled water, by acidifying. Thus k_{gas} approaches zero with the completeness with which the carbon dioxide has been driven out of solution.

In view of the findings in this investigations, published values for k_{gas} at various temperatures for distilled water and waters con-

taining certain amounts of neutral salts cannot be used in this method in determining the carbon dioxide tensions of natural waters except in neutral waters. The assumption that the carbon dioxide dissolves in the dilute solution of bicarbonates in the same proportions as in distilled water or in water free from bicarbonates seemingly does not hold. In using the field method for determining the carbon dioxide tensions of natural waters as described by Powers (1927) and Powers and Bond (1927 and 1928) the k_{gas} , that is, Kk_{gas} , must be determined in the field for each natural water.

CONCLUSIONS

1. The carbon dioxide tensions of natural waters can be determined colorimetrically or electrometrically in the field. Organic matter in solution seemingly does not interfere.
2. In order to obtain absolute and not relative values for the carbon dioxide tensions of natural waters the actual carbon dioxide partial pressure of the air used for aeration must be known.
3. The assumption that is sometimes made that the carbon dioxide dissolves in the dilute solution of bicarbonates in the same proportions as in distilled water or in water free from bicarbonates seemingly does not hold.

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Pinnotheridae of Puget Sound

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The purpose of this paper is to furnish keys, comparison and descriptive material for the Pinnotheridae occurring in the Puget Sound waters, together with illustrations of the Pinnotherid crabs and of the hosts with which they live commensally.

The paper is based on material collected from 1925 to 1928 in the Friday Harbor region, and on material collected over a number of years by Professor Trevor Kincaid of the University of Washington, under whose direction the work was done.

In the preparation of this paper the works of Rathbun (1918) and of Way (1917) were especially helpful. Miss Rathbun has very kindly given advice and has verified the identification of species. Acknowledgments are also due Dr. John E. Guberlet and Miss Belle A. Stevens, both of the University of Washington; and Dr. T. C. Frye, Director of the Puget Sound Biological Station, where the collecting and much of the work were done.

The color descriptions are based on crabs preserved in four per cent formalin.

The Pinnotherid crabs of the Puget Sound region fall into four genera in two subfamilies as given below:

- Family: Pinnotheridae
 - Subfamily: Pinnotherinae
 - Genus: Pinnotheres
 - Genus: Fabia
 - Subfamily: Pinnotherelinae
 - Genus: Pinnixa
 - Genus: Scleroplax

Family PINNOTHERIDAE Dana

Carapace somewhat quadrilateral, more or less rounded, usually more or less membranous; front, orbits and eye stalks very small; antero-lateral margins entire. Abdomen of female frequently as large as carapace; abdomen of male very narrow. Male openings sternal. Males frequently smaller than females. Small symbiotic crabs, living in bivalve mollusc shells, worm tubes, tunicates, echinoderms, or rarely free.

KEY TO GENERA

A. Carapace little if any wider than long.

B. Carapace hard in both male and female, smoothly convex from elevated center to all margins; 3rd walking leg longest.

Scleroplax, p. 304

BB. Carapace soft in female, hard in male, not smoothly convex from elevated center to all margins but with antero-lateral margins either high or defined by ridge rimmed with coarse setae; 2nd or 4th walking legs longest.

C. With longitudinal sulcus extending backward from upper margin of each orbit and enclosing median area.

Fabia, p. 286

CC. Without longitudinal sulci.

Pinnotheres, p. 285AA. Carapace at least $1\frac{1}{2}$ times as wide as long. *Pinnixa*, p. 289

COMPARISON OF SPECIES OF PINNOTHERIDAE	<i>Pinnothores pugettensis</i>	<i>Fabia subquadrata</i>	<i>Scleroplax granulata</i>	<i>Pinnixa</i>				
				<i>fabia</i>	<i>littoralis</i>	<i>tubicola</i>	<i>schmitti</i>	<i>clarna</i>
Length of carapace less than $\frac{2}{3}$ of width	+	+	+	-	-	-	-	-
Longest walking leg	4th	2nd	3rd	3rd	3rd	3rd	3rd	3rd
Longitudinal sulci extending back from orbits	-	+	-	-	-	-	-	-
Dactyls of 3rd walking legs strongly falcate	-	-	-	+	+	-	-	-
Outer margin of orbit oval or angled	o	o	o	o	a	o	o	o
Fingers of female gaping when closed	-	-	-	-	+	-	-	-
Dactyls of 3rd and 4th walking legs much shorter than those of 1st and 2nd	-	+	-	-	-	+	-	-
Fingers crossing when closed	-	+	+	-	-	-	+	+
Dactyls of 2nd and 3rd walking legs at least 1.5 times the length of those of the 1st and 4th	-	-	-	-	-	-	+	+
Inner margin of movable finger with tooth, doubtful or none	d	t	n	t	n	t	t	n
Ratio of width to length of carapace								
in male		1.04	1.34	1.71	1.89	2.1	1.84	1.85
in female	1.05	1.25	1.41	1.59	1.59	2.5	1.6	2.28

Genus PINNOTHERES Latreille

Carapace smooth, membranous or hard, suborbicular, without longitudinal sulci behind orbits. Outer maxilliped with ischium rudimentary, merus large; palp usually of three joints of which the last is attached to the preceding joint on its inner margin or at its antero-external angle. Walking legs of moderate length and subequal.

Pinnotheres pugettensis Holmes. Figs. 1-3

Pinnotheres pugettensis Holmes, Occas. Papers Calif. Acad. Sci. 7:86. 1900.
Rathbun, Bull. U. S. Nat. Mus. 97:82. 1918.

Description of female. Carapace soft, subpentagonal, widest anteriorly; front slightly arcuate; orbits subcircular. Terminal joint of

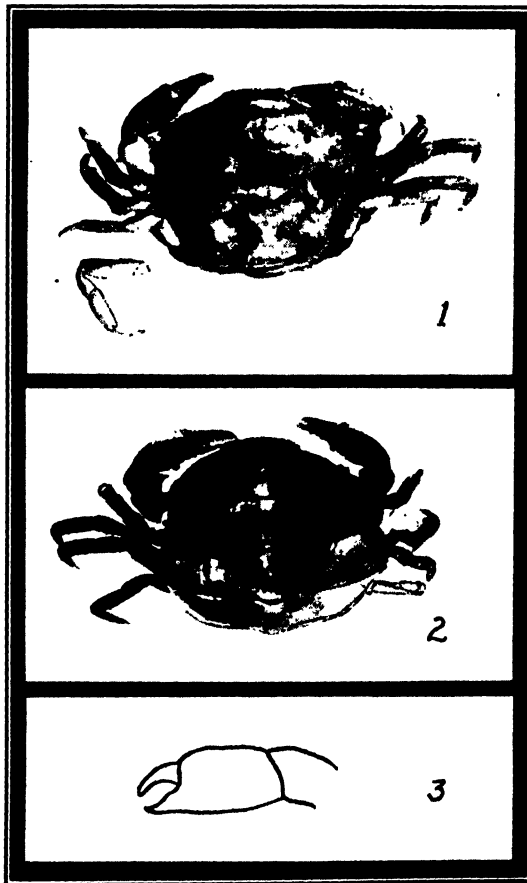


Fig. 1. *Pinnotheres pugettensis*, female; dorsal view, $\times 2.5$
Fig. 2. *Pinnotheres pugettensis*, female; ventral view, $\times 2.5$
Fig. 3. *Pinnotheres pugettensis*, female; left chela, outer view, $\times 8$

outer maxilliped small, attached distally to middle of propod. Chela stout; margins of hand widening distally; fingers subcylindrical, straight with incurving tips; fixed finger with low prominent tooth near middle of inner margin. Walking legs slender, order of length 4, 3, 2, 1.

Male unknown.

Color. Light reddish brown with tinge of purple; external palm with two streaks of a lighter shade.

Dimensions. Length of carapace 10 mm, width of same 10.5 mm.

Range. Departure Bay, British Columbia to Puget Sound.

Habitat. In tunicates.

Local distribution. In *Tethyum aurantium* (Pallus) collected by Professor Trevor Kincaid in the Friday Harbor region; none were collected by the writer.

Genus *FABIA* Dana

Carapace smooth, membranous, subquadrate, with longitudinal sulci leading back from upper margin of orbits and enclosing median area. Outer maxilliped with ischium rudimentary and merus large, last joint of palp attached to preceding one on inner margin. Legs slender; 2nd walking leg longest.

Fabia subquadrata Dana. Figs. 4-9

Female

Fabia subquadrata Dana, Proc. Acad. Nat. Sci. Phila. 5:253. 1851; Crustacea U. S. Expl. Exped. 1:382. 1852. Holmes, Occas. Papers Calif. Acad. Sci. 7: 87. 1900 (part).

Raphonotus subquadratus Rathbun, H. A. E. 10:186. 1904. Weymouth, Stanford Univ. Publ., Univ. Ser. no. 4:55. 1910.

Fabia subquadrata Rathbun, Bull. U. S. Nat. Mus. 97:102. 1918. Schmitt, Univ. of Calif. Publ. in Zool. 23:253. 1921.

Male

Cryptophrys concharum Rathbun, Proc. U. S. Nat. Mus. 16:250. 1893. Holmes, Occas. Papers Calif. Acad. Sci. 7:96. 1900. Rathbun, H. A. E. 10:188. 1904. Weymouth, Stanford Univ. Publ., Univ. Ser. no. 4:60. 1910.

Pinnotheres concharum Rathbun, Bull. U. S. Nat. Mus. 97:86. 1918. Schmitt, Univ. of Calif. Publ. in Zool. 23:252. 1921.

Description of female. Carapace subquadrilateral, membranous, smooth, marked with longitudinal sulci leading back from middle of upper margin of orbits, narrowing posteriorly and enclosing the median area; front smoothly rounded, and usually with shallow,

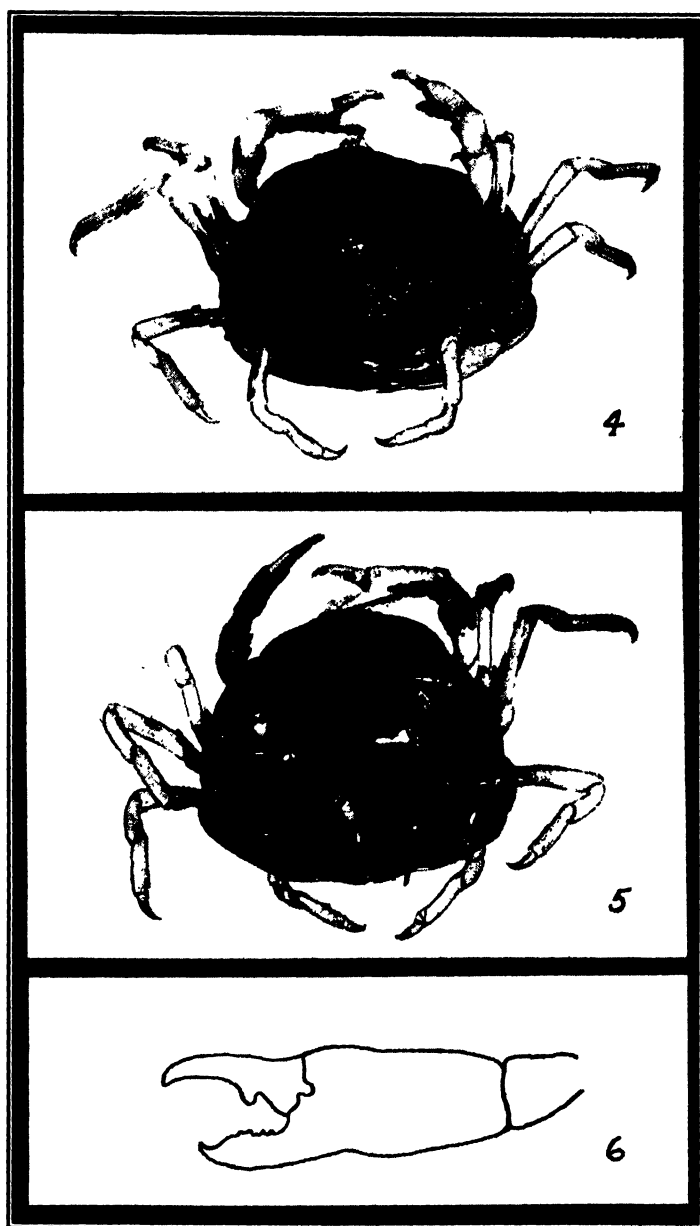


Fig. 4. *Fabia subquadrata*, female; dorsal view, $\times 2$

Fig. 5. *Fabia subquadrata*, female; ventral view, $\times 2$

Fig. 6. *Fabia subquadrata*, female; left chela, outer view, $\times 8$

transverse, pubescent sulcus running between the upper line of the orbits. Terminal joint of outer maxilliped small, attached near middle of inner margin of propod. Chela smooth; palms widening slightly

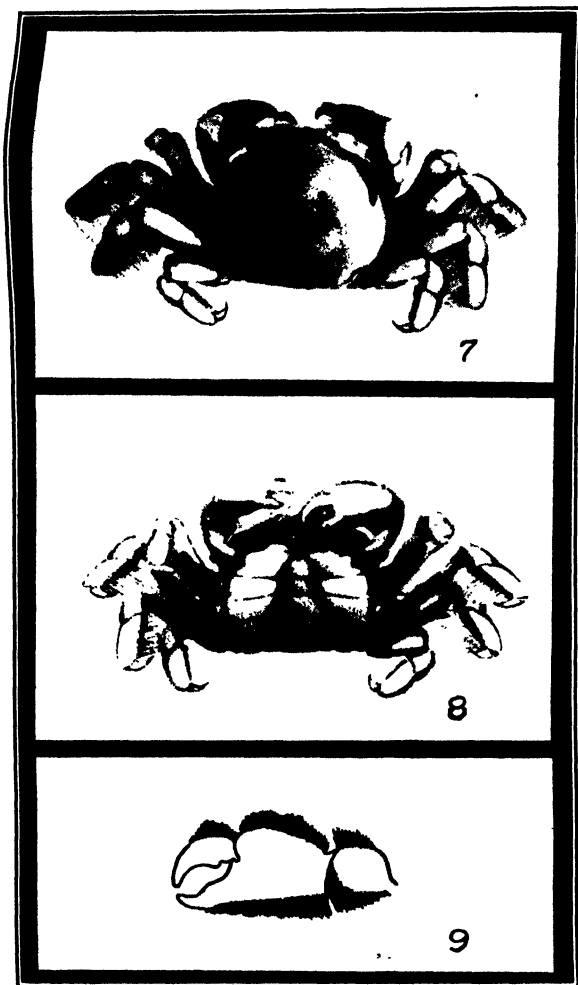


Fig. 7. *Fabia subquadrata*, male, dorsal view, $\times 3.5$
Fig. 8. *Fabia subquadrata*, male; ventral view, $\times 3.5$
Fig. 9. *Fabia subquadrata*, male; left chela, outer view, $\times 8$

to distal end, inner surface hairy with two rows of hairs, the innermost extending to end of fixed finger; fingers slightly curved, movable finger with prominent tooth near middle of inner margin. Walking legs slender, order of length 2, 3, 1, 4.

Description of male. Carapace subpentagonal, hard, slightly longer than wide; anterior and antero-lateral margins defined by a rim of coarse setae which are thickest and longest at the antero lateral angles; orbits circular. Abdomen and sternum smooth; abdomen constricted between last two segments. Chela stout, margined with hair; fingers incurved at distal end, dorsal margin of propods of 2nd and 3rd walking legs thickly margined with hair which is bent downward and whose length exceeds the width of the propod. Order of length of walking legs 2, 3, 1, 4.

Color. Female: digestive glands and alimentary canal appear orange-yellow, remainder a grayish white; male: a tawny ochraceous on anterior half of carapace, shading to paler tint on posterior carapace and legs.

Dimensions. Female: length of carapace 10 mm, width of same 12.5 mm. Male: length of carapace 7 mm, width of same 7.3 mm.

Range. Alaska to San Diego, California.

Habitat. Commensal in bivalve molluscs and ascidians. Male frequently free swimming.

Local distribution. In *Modiolus modiolus*, off Flat Top Island at 220 meters; off Brown Island at 40 meters and 100 meters; in *Mytilus edulis* in lagoon on Blakely Island; in *Mytilus californicus* at Cattle Point; and frequently free in trawl. One immature female in branchial sac of tunicate *Styela gibbsii* (Stimpson). Collected in *Venericardia ventricosa* by Professor Trevor Kincaid off O'Neal Island in 1921.

Remarks. Immature females strongly resemble adult males. Membranous carapace of recently molted males marked with the two longitudinal sulci which lead back from middle of upper margin of orbits but which become obscure with the hardening of the carapace.

Genus PINNIXA White

Carapace wider than long, more or less membranous. Ischium of outer maxilliped small, merus large, palp attached near base of inner margin of preceding joint. Third pair of walking legs longer and stronger than others.

KEY TO SPECIES

- A. Dactyls of 3rd walking legs with corneous tips strongly falcate.
- B. Fingers of chela incurved at tip to form gap when closed;

- outer margin of orbits angular. *P. littoralis*, p. 293
- BB. Fingers of chela not incurved to form gap when closed;
outer margin of orbits rounded. *P. fabia*, p. 290
- AA. Dactyls of 3rd walking legs with corneous tips not strongly
falcate, but continuing line of dactyl.
- C. Dactyls of 3rd and 4th walking legs much shorter than those
of the 1st and 2nd. *P. tubicola*, p. 301
- CC. Dactyls of 3rd and 4th walking legs subequal to those of the
1st and 2nd.
- D. With tooth near middle of inner margin of movable finger;
with low ridge extending forward to antero-lateral margin
from either end of cardiac ridge. *P. schmitti*, p. 296
- DD. Without tooth on inner margin of movable finger; no such
ridge as in D, carapace smooth to lateral margin.
P. eburna, p. 298

Pinnixa faba (Dana). Figs. 10-16

Pinnotheres faba Dana, Proc. Acad. Nat. Sci. Phila. 5:253. 1851. Crust. U. S. Expl. Exped. 1:381. 1852.

Pinnixa faba Holmes, Occas. Papers Calif. Acad. Sci. 7:93. 1900. Rathbun, H. A. E. 10:188. 1904. Weymouth, Stanford Univ. Publ., Univ. Ser. no. 4:59. 1910 (part). Rathbun, Bull. U. S. Nat. Mus. 97:142. 1918. Schmitt, Univ. Calif. Publ. in Zool. 23:259. 1921.

Description of female. Carapace oval, uneven, membranous, with deep median groove extending back from interorbital area; gastric region high, sloping gently to posterior margin. Chela large; palms sub-oblong, widening distally; fingers not gaping when closed; movable finger with low tooth on inner margin near base.

Description of male. Carapace hard, less uneven than in female, median groove slight. Chela stouter; movable finger with triangular tooth on inner margin near base; fixed finger horizontal, notched distally to receive movable finger which is strongly deflexed, leaving gap when closed; merus of 3rd walking leg more than twice as long as wide. Order of length of walking legs 3, 2, 1, 4.

Color. Orange chrome with grayish white patches over median branchial region of male.

Dimensions. Female: length of carapace 15.2 mm, width of same 22.8 mm. Male: length of carapace 7.6 mm, width of same 13 mm.

Range. Alaska to Humboldt Bay, California (Rathbun), to San Diego, California (Holmes).

Habitat. Commensal in clams.

Local distribution. Adults of both sexes common together in *Schizothaerus nuttallii*. Material collected from False Bay, San Juan Island; Flat Point, Lopez Island; East Sound, Orcas Island; and

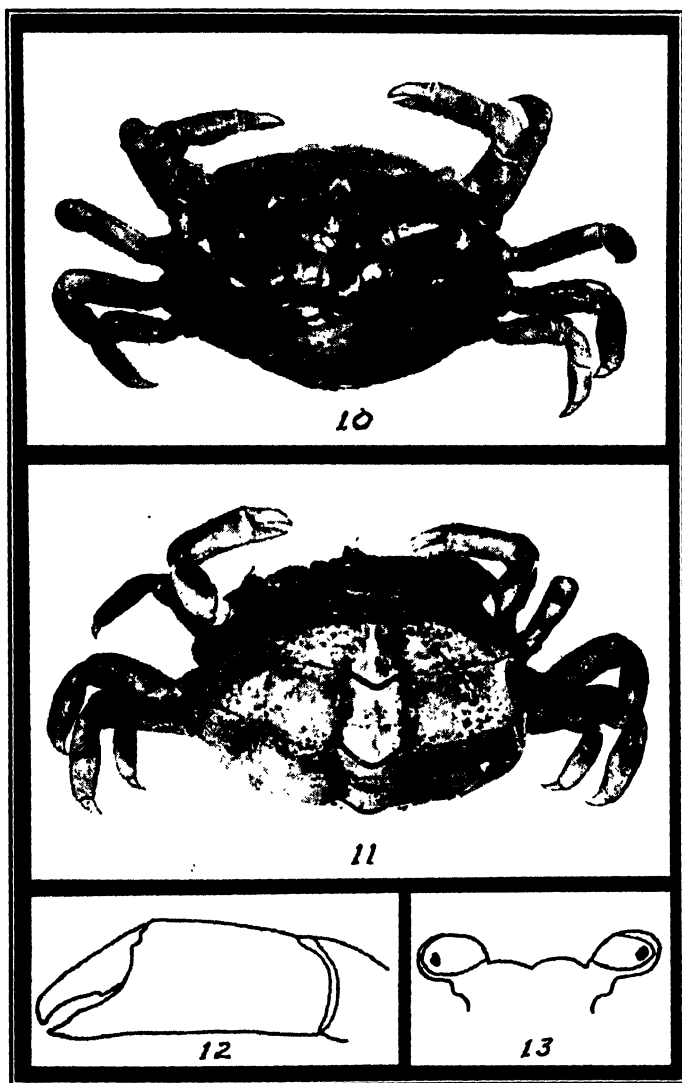


Fig. 10. *Pinnixa faba*, female; dorsal view, $\times 2$

Fig. 11. *Pinnixa faba*, female; ventral view, $\times 2$

Fig. 12. *Pinnixa faba*, female; left chela, outer view, $\times 8$

Fig. 13. *Pinnixa faba*, female; orbits, $\times 8$

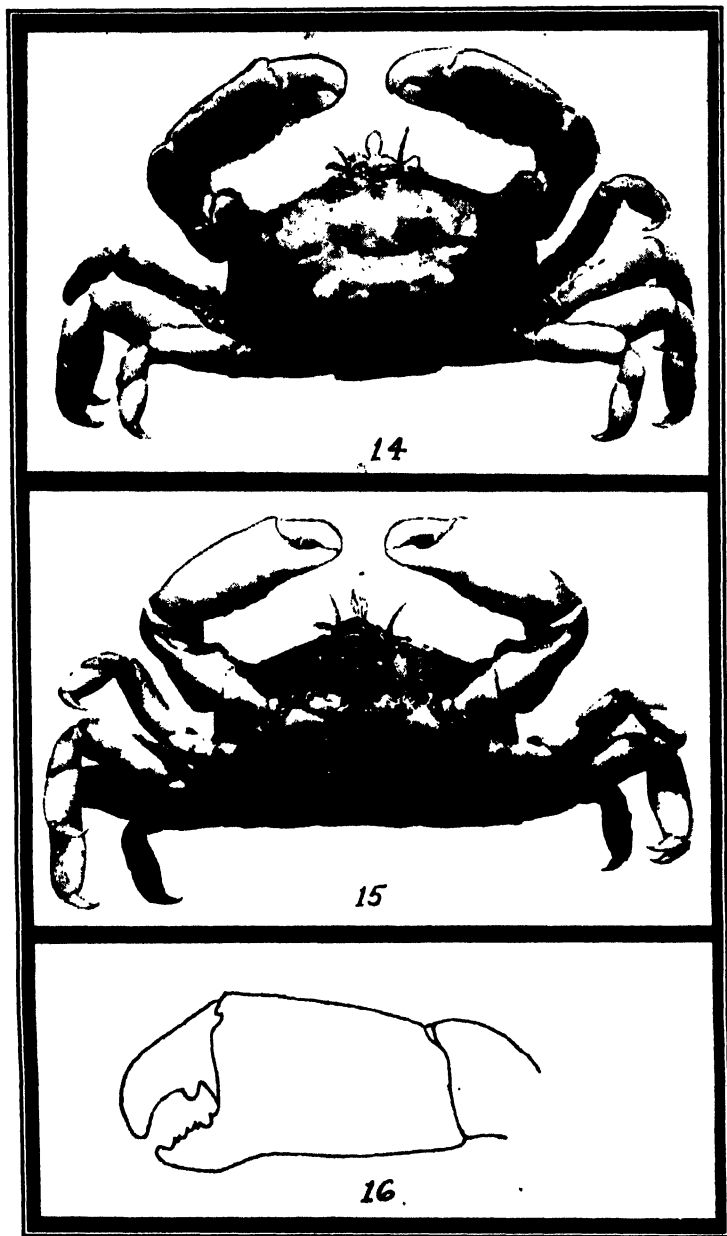


Fig. 14. *Pinnixa faba*, male; dorsal view, $\times 3$

Fig. 15. *Pinnixa faba*, male; ventral view, $\times 3$

Fig. 16. *Pinnixa faba*, male; left chela, outer view, $\times 8$

Poulsbo; all in Washington. Young of both sexes and small males are common in *Macoma nasuta*, *M. inquinata*, *M. indentata*, *M. secta*, *Mya arenaria*, *Saxodomus giganteus* and *Schizothaerus nuttallii*; and were found rarely in *Cardium corbis* and *Lyonsia saxicola*. One small male was found in the atrial cavity of the tunicate, *Styela gibbsii* (Stimpson). The species is commonly found with *Pinnixa littoralis*.

Pinnixa littoralis Holmes. Figs. 17-23, 48-60

Pinnixa littoralis Holmes, Proc. Calif. Acad. Sci. (2) 4:571. 1894; Occas. Papers Calif. Acad. Sci. 7:91. 1900. Rathbun, H. A. E. 10:188. 1904. Weymouth, Stanford Univ. Publ., Univ. Ser. no. 4:58. 1910 (part). Way, Puget Sd. Mar. Sta. Publ. 1:362. 1917. Rathbun, Bull. U. S. Nat. Mus. 97:145. 1918. Nininger, Jour. Ent. Zool. Pomona Coll. 10:41. 1918. Schmitt, Univ. Calif. Publ. in Zool. 23:260. 1921.

Description of female. Carapace oval, membranous, somewhat pointed at sides, surface uneven, gastric region with deep longitudinal median groove, median area of branchial region depressed, front evenly rounded; orbits oval but with acute angle at outer margin, as seen from above only slightly visible. Chela large; palms suboblong, widening a little distally; fingers crossed at tips, gaping when closed; movable finger without tooth near base; fixed finger with shallow notch at tip; corneous tips of dactyls of walking legs strongly falcate. Order of length of walking legs 3, 2, 1, 4.

Description of male. Carapace hard, less uneven than in female, median groove slight. Inner margin of dactyl of chela entire. Third walking leg noticeably stoutest, merus twice as long as wide.

Color. Female: yellowish white with yellow-orange patches on anterior part of carapace; male: yellowish white with brownish yellow on propods of walking legs.

Dimensions. Female: length of carapace 16.3 mm, width of same 26 mm. Male: length of carapace 7.4 mm, width of same 14 mm.

Range. Alaska to San Diego, California.

Habitat. Commensal in clams.

Local distribution. Adult females and males are common together in *Schizothaerus nuttallii*. Material collected from False Bay, San Juan Island; Flat Point, Lopez Island; East Sound, Orcas Island; and Poulsbo, Washington. Young of both sexes and small males are common in *Macoma nasuta*, *M. inquinata*, *M. secta*, *M. indentata*, *Mya arenaria*, *Saxodomus giganteus* and *Schizothaerus nuttallii*; and were rarely found in *Cardium corbis*, *Serripes groenlandicus* and *Lyonsia saxicola*. The species is commonly found with *Pinnixa faba*.

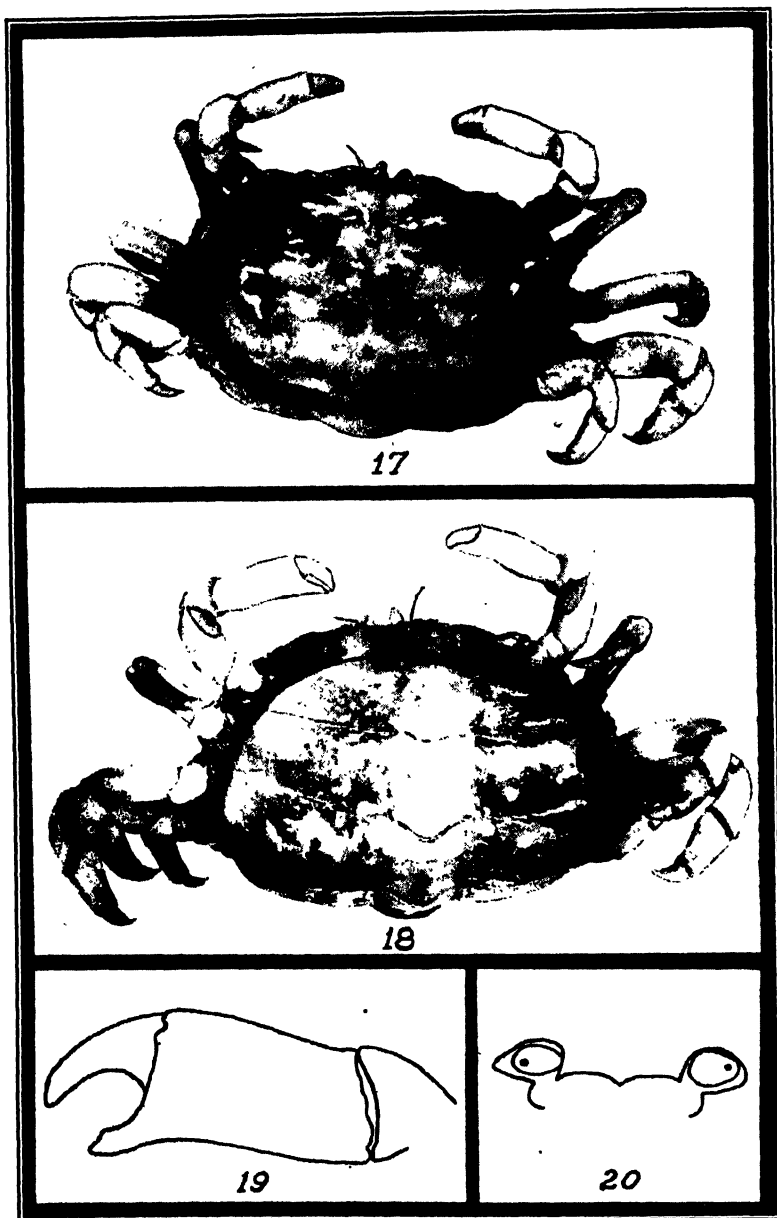


Fig. 17. *Pinnixa littoralis*, female; dorsal view, $\times 1.5$

Fig. 18. *Pinnixa littoralis*, female; ventral view, $\times 1.5$

Fig. 19. *Pinnixa littoralis*, female; left chela, outer view, $\times 8$

Fig. 20. *Pinnixa littoralis*, female; orbits, $\times 8$

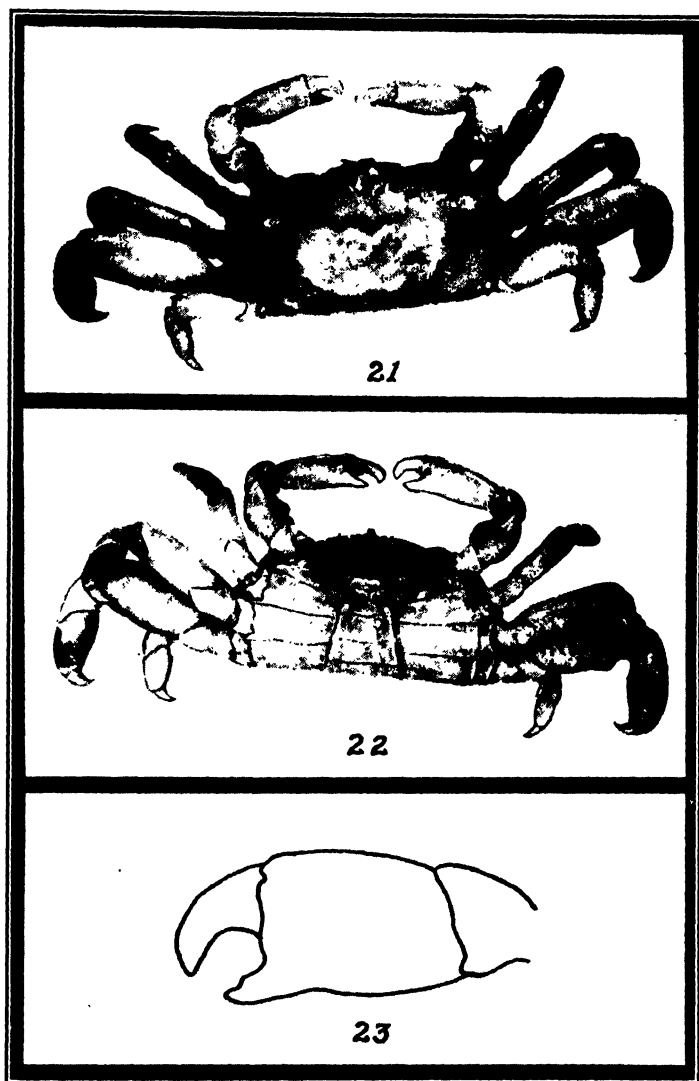


Fig. 21. *Pinnixa littoralis*, male; dorsal view, $\times 2$

Fig. 22. *Pinnixa littoralis*, male; ventral view, $\times 2$

Fig. 23. *Pinnixa littoralis*, male; left chela, outer view, $\times 8$

Pinnixa schmitti Rathbun. Figs. 24-29

Pinnixa occidentalis Rathbun, H. A. E. 10:187. 1904 (part).

Pinnixa schmitti Rathbun, Bull. U. S. Nat. Mus. 97:162. 1918. Schmitt, Univ. of Calif. Publ. in Zool. 23:264. 1921.

Description. Carapace oblong, hard, smooth; antero-lateral margin ridged, tuberculate; gastric region with slight median groove; cardiac ridge low, rounded, transverse, with a smooth ridge running forward from each end to middle of antero-lateral margin. Palm oblong, margins slightly convex; fixed finger short, horizontal; movable

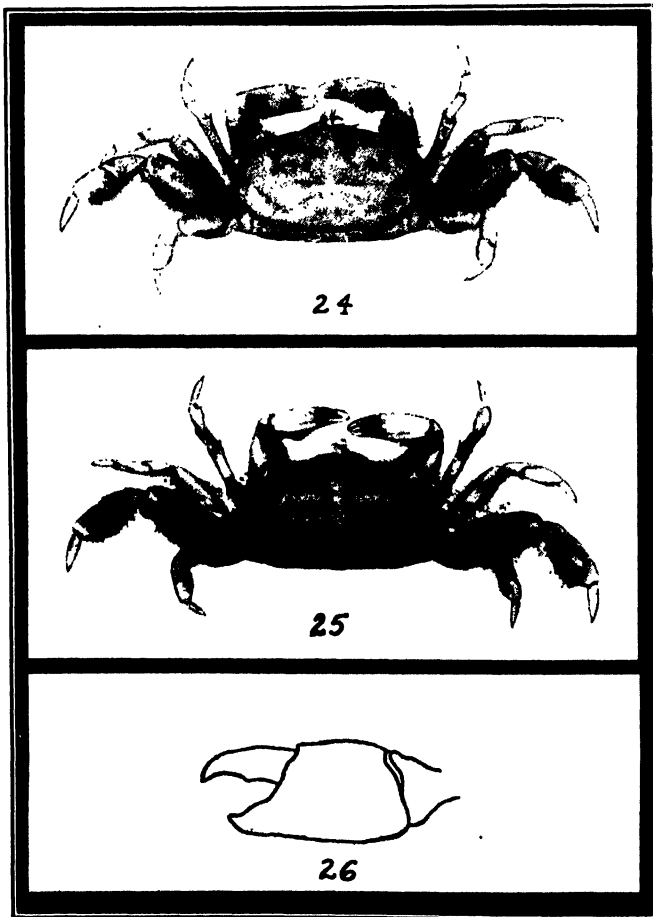


Fig. 24. *Pinnixa schmitti*, female; dorsal view, $\times 3.3$
Fig. 25. *Pinnixa schmitti*, female; ventral view, $\times 3.3$
Fig. 26. *Pinnixa schmitti*, female; left chela, outer view, $\times 8$

finger deflexed downward slightly in female, not gaping when closed; low tooth about middle of each finger on inner margin; movable finger more abruptly deflexed in male and gaping when closed. Order of length of walking legs 3, 2, 1, 4; dactyls about as long as propods, almost straight.

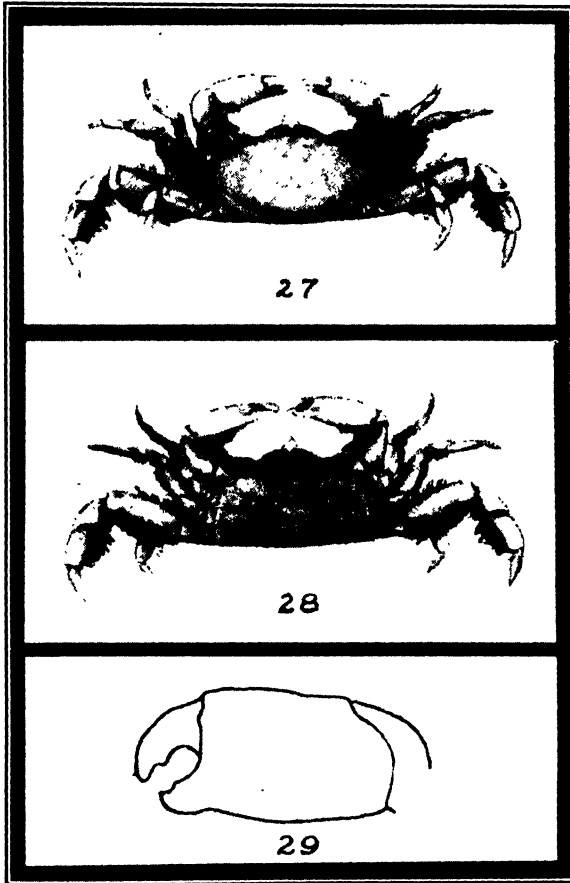


Fig. 27. *Pinnixa schmitti*, male; dorsal view, $\times 3.2$

Fig. 28. *Pinnixa schmitti*, male; ventral view, $\times 3.2$

Fig. 29. *Pinnixa schmitti*, male; left chela, outer view, $\times 8$

Color. Dirty yellowish white.

Dimensions. Female: length of carapace 5 mm, width of same 8 mm. Male: length of carapace 5 mm, width of same 9.2 mm.

Range. Alaska to San Francisco Bay, California.

Habitat. In burrows of Upogebia.

Local distribution. In burrows of Upogebia on beach 1.2 miles southeast of Friday Harbor, Minnesota Reef and False Bay, San Juan Island; and on Blakely Island.

Remarks. *P. schmitti* was found near the top of the burrow of Upogebia just below the plug of loose gravel with which the burrow is closed. The Upogebia burrow is described by Belle A. Stevens in a paper on Callianassidae to appear in Publ. Puget Sound Biol. Sta. Vol. 6.

Pinnixa eburna, new species. Figs. 30-35

Description. Carapace hard, smooth, polished, subelliptic, with broad posterior margin, flattened on top and truncate at sides, margined with coarse setae; gastric and cardiac regions separated by a deep, curved depression; antero-lateral ridge smooth, becoming more prominent anteriorly and extending to a point just posterior to the

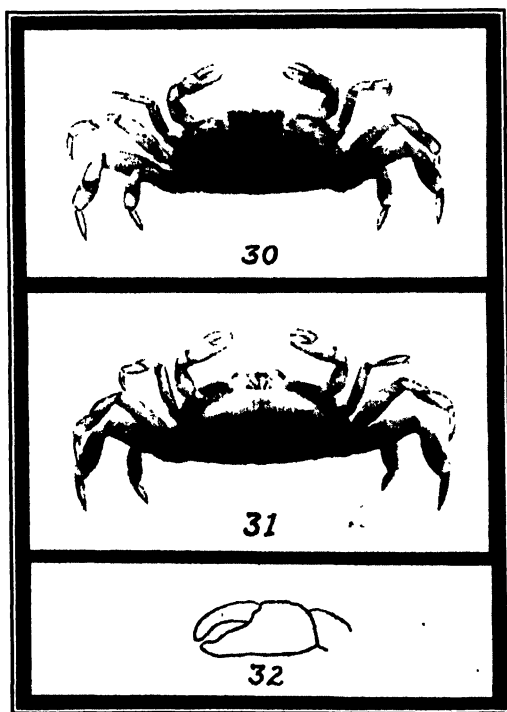


Fig. 30. *Pinnixa eburna*, female; dorsal view, $\times 3.3$
Fig. 31. *Pinnixa eburna*, female; ventral view, $\times 3.3$
Fig. 32. *Pinnixa eburna*, female; left chela, outer view, $\times 8$

outer margin of the orbit. Eyes as seen from above set in semi-circular orbits, between which front extends to general curve of anterior margin, front slightly deflexed and with slight median groove; eye stalks very stout, filling circular orbits. Antenna equal in length to interorbital space. Last joint of outer maxilliped elongate-spatulate, equaling length of propod near base of which it

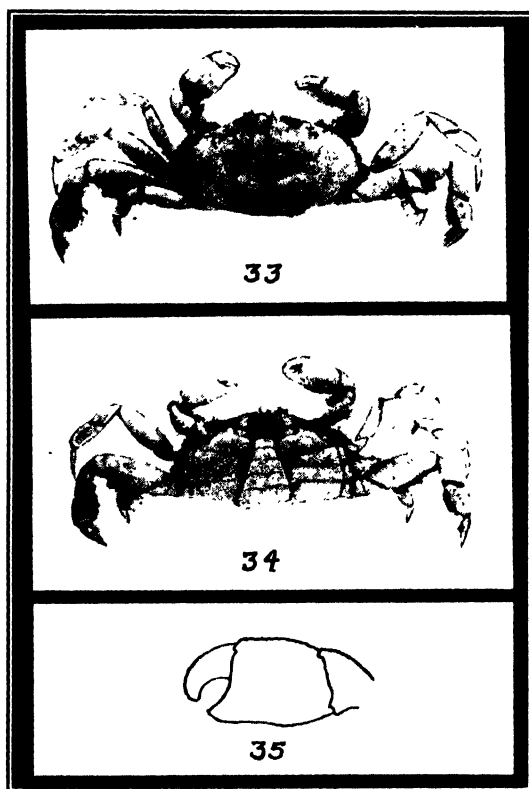


Fig. 33. *Pinnixa eburna*, male; dorsal view, $\times 3.3$

Fig. 34. *Pinnixa eburna*, male; ventral view, $\times 3.3$

Fig. 35. *Pinnixa eburna*, male; left chela, outer view, $\times 8$

is attached. Chela swollen; palm smooth, suboblong, margins convex; fixed finger stout, triangular, with horizontal lower margin rolled outward to form thickened margin above which is a line of sparsely set, coarse, short setae; movable finger longer than fixed finger, curving abruptly downward, not gaping when closed, with tooth near middle of inner margin; tips of fingers crossing. Order of length of

walking legs 3, 2, 1, 4; dactyls styliform, almost straight, dactyl of 2nd leg longest and subequal to its propod in length; 3rd and 4th

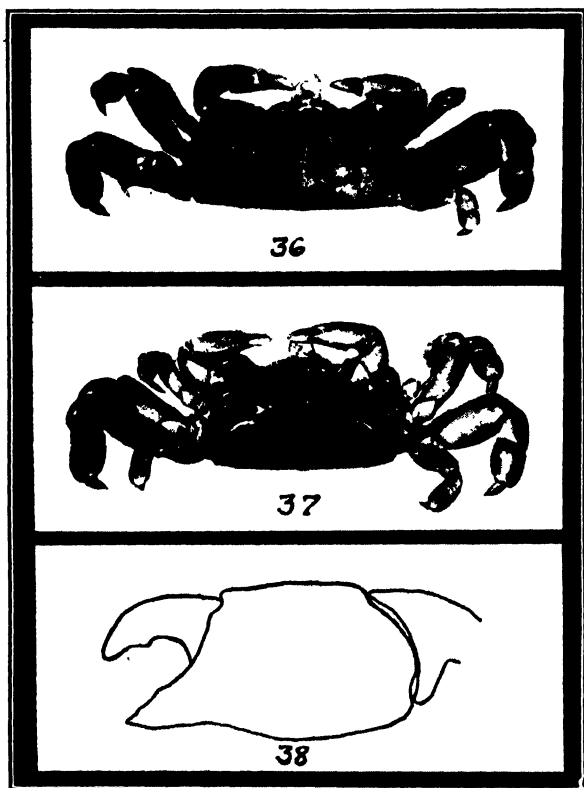


Fig. 36. *Pinnixa tubicola*, female; dorsal view, $\times 2.5$

Fig. 37. *Pinnixa tubicola*, female; ventral view, $\times 2.5$

Fig. 38. *Pinnixa tubicola*, female; left chela, outer view, $\times 8$

legs, and; merus of 1st and 2nd legs margined with coarse, plumose hairs, which are thicker and longer on posterior legs.

Color. Varies from ivory white with yellowish tinge on carapace to mottled orange-yellow.

Dimensions. Female: length of carapace 3.5 mm, width of same 8 mm. Male: length of carapace 3.5 mm, width of same 6.5 mm.

Habitat. Tubes of *Arenicola* worms.

Local distribution. False Bay, San Juan Island, on beach exposed by tides lower than 1.0 foot.

Type locality. False Bay, San Juan Island; in tube with *Arenicola*. The holotype male, has been deposited in United States Na-

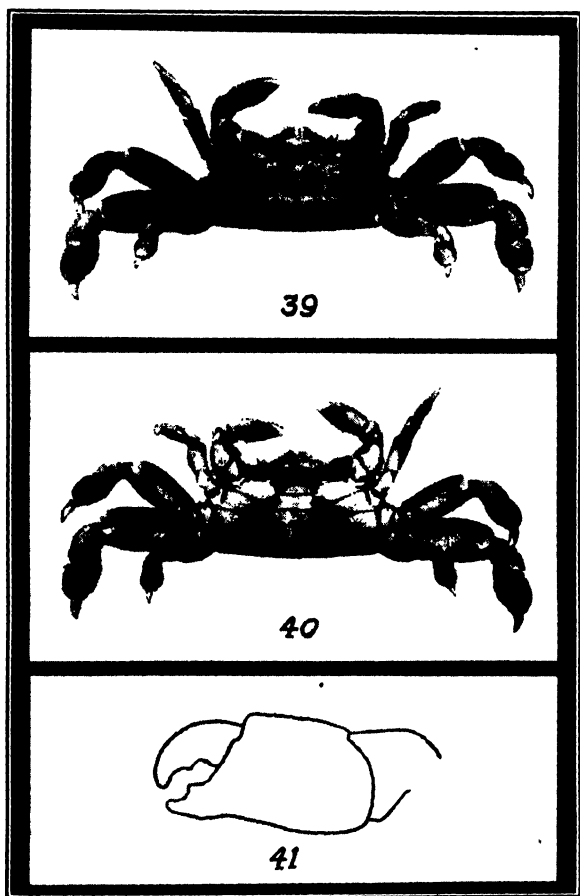


Fig. 39. *Pinnixa tubicola*, male; dorsal view, $\times 3$

Fig. 40. *Pinnixa tubicola*, male; ventral view, $\times 3$

Fig. 41. *Pinnixa tubicola*, male; left chela, outer view, $\times 8$

tional Museum (Cat. No. 61786); paratype, female, (Cat. No. 61787).

Pinnixa tubicola Holmes. Figs. 36-41

Pinnixa tubicola Holmes, Proc. Calif. Acad. Sci. (2) 4:569. 1894; Occas. Papers Calif. Acad. Sci. 7:91. 1900. Rathbun, H. A. E. 10:187. 1904. Weymouth, Stanford Univ. Publ., Univ. Ser. no. 4:57. 1910. Way, Puget Sd. Mar. Sta. Publ. 1:361. 1917. Rathbun, Bull. U. S. Nat. Mus. 97:165. 1918. Schmitt, Univ. of Calif. Publ. in Zool. 23:265. 1921.

Description. Carapace elongate-oval, hard, smooth; outer portion of antero-lateral margin slightly ridged; ridge more pronounced

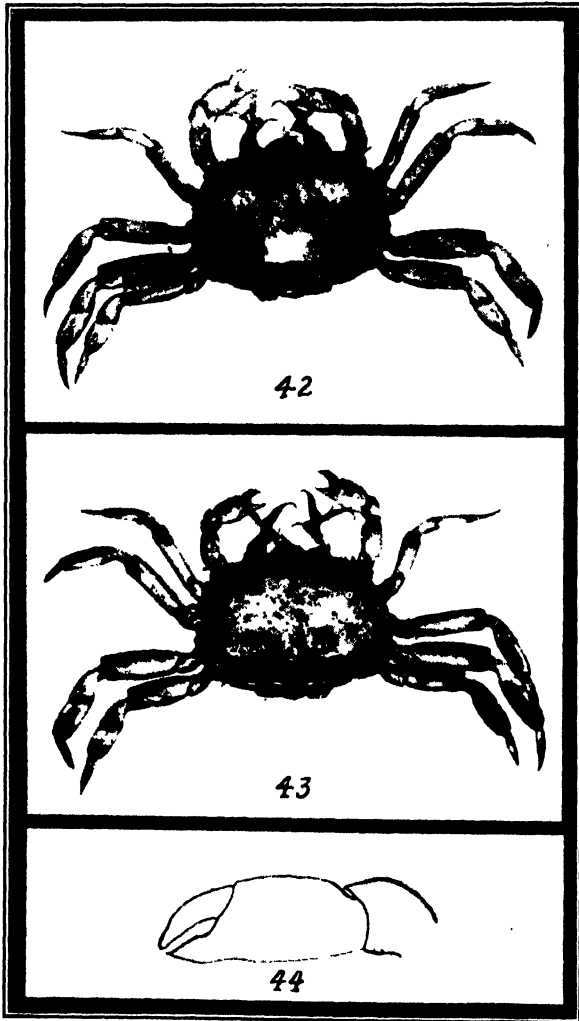


Fig. 42. *Scleroplax granulata*, female; dorsal view, $\times 2.5$
Fig. 43. *Scleroplax granulata*, female; ventral view, $\times 2.5$
Fig. 44. *Scleroplax granulata*, female; left chela, outer view, $\times 8$

in male. Chela smooth; palm narrowing distally, lower margin very convex and upper margin slightly so, especially near attachment with carpus; fingers short, each with small tooth near middle of inner mar-

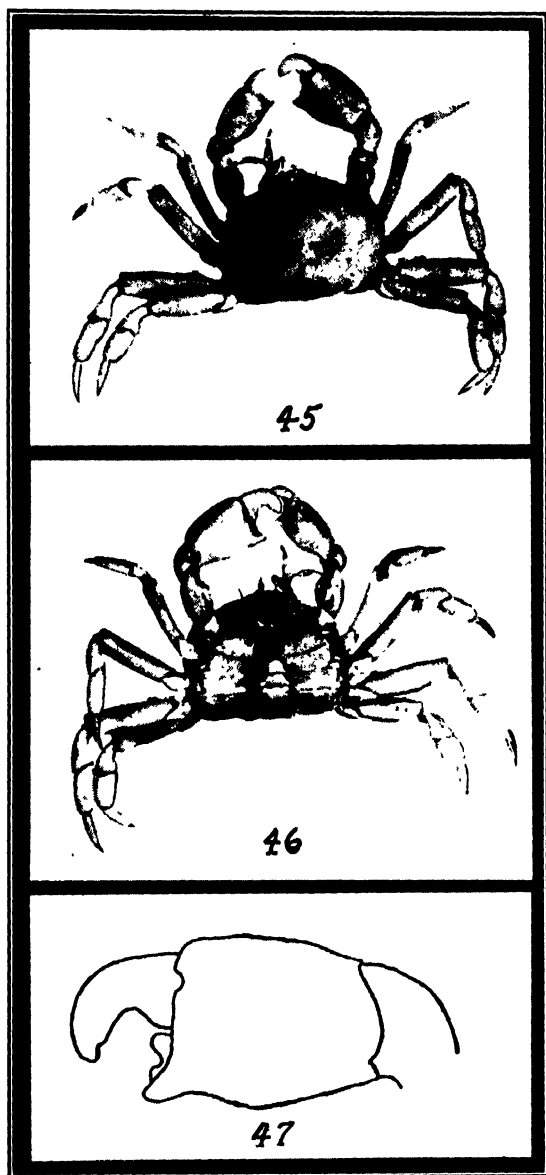


Fig. 45. *Scleroplax granulata*, male; dorsal view, $\times 2.5$
Fig. 46. *Scleroplax granulata*, male; ventral view, $\times 2.5$
Fig. 47. *Scleroplax granulata*, male; left chela, outer view, $\times 8$

gin, tips crossing when closed. Order of length of walking legs 3, 2, 1, 4; 4th leg very short, scarcely reaching distal end of merus of 3rd; propod of 3rd and 4th legs subquadrate, distal end much wider than base of dactyl.

Color. Female: yellowish orange; male: reddish orange. Each has lighter markings on carapace.

Dimensions. Female: length of carapace 4 mm, width of same 10 mm. Male: length of carapace 3.2 mm, width of same 6.8 mm.

Range. Puget Sound to San Diego, California.

Habitat. Usually found in leathery tubes of annelids (Holmes).

Local distribution. Found in tubes of Amphitrite worms on beach on west side of Brown Island and at False Bay, San Juan Island.

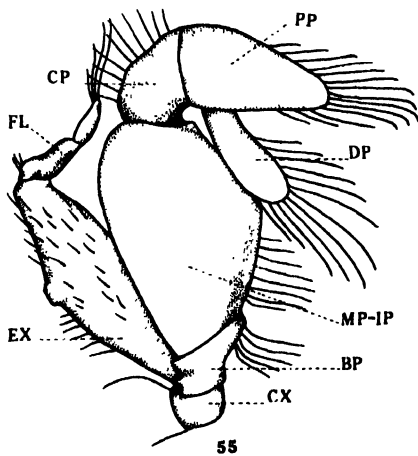
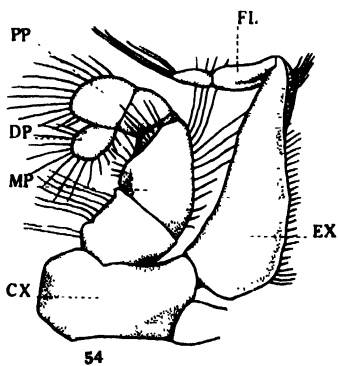
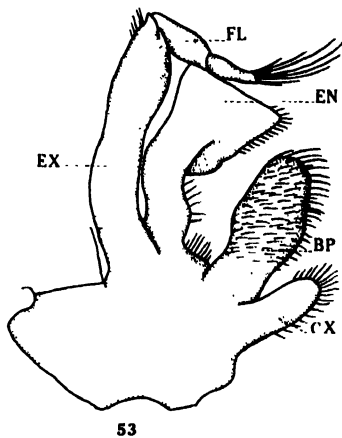
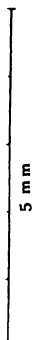
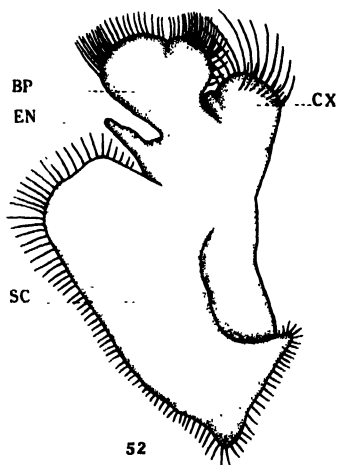
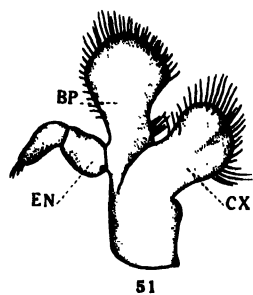
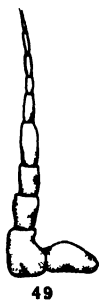
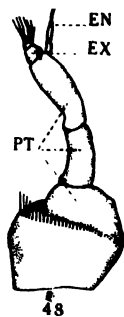
Genus SCLEROPLAX Rathbun

Carapace transverse, hard, very convex. Outer maxilliped with ischium rudimentary, merus longer than broad, last joint of palp attached near proximal end of inner margin of preceding joint. Walking legs similar, slender, 3rd pair longest.

PINNIXA LITTORALIS, FEMALE

BP - basipodite	FL - flagellum
CP - carpopodite	IP - ischiopodite
CX - coxopodite	MP - meropodite
DP - dactylopodite	PP - propodite
EN - endopodite	P'T - protopodite
EP - epipodite	MDP - mandibular palp
EX - exopodite	

- Fig. 48. Right antennule, lateral
- Fig. 49. Right antenna, lateral
- Fig. 50. Right mandible, ventral
- Fig. 51. Right first maxilla, ventral.
- Fig. 52. Right second maxilla, ventral
- Fig. 53. Right first maxilliped, ventral
- Fig. 54. Right second maxilliped, dorsal
- Fig. 55. Right third maxilliped, ventral



Scleroplax granulata Rathbun. Figs. 42-47

Scleroplax granulata Rathbun, Proc. U. S. Nat. Mus. 16:251. 1893.

Pinnixa (*Scleroplax*) *granulata* Holmes, Occas. Papers Calif. Acad. Sci. 7:94. 1900.

Scleroplax granulata Rathbun, H. A. E. 10:188. 1904. Weymouth, Stanford Univ. Publ., Univ. Ser. no. 4:59. 1910. Way, Puget Sd. Mar. Sta. Publ. 1:362. 1917. Rathbun, Bull. U. S. Nat. Mus. 97:171. 1918. Schmitt, Univ. of Calif. Publ. in Zool. 23:267. 1921.

Description. Carapace subpentagonal, hard, elevated in center and sloping convexly to all margins; front advanced between orbits to general curve of anterior margin. Last two joints of outer maxilliped elongate and subequal in length. Chela of female weak; fixed finger horizontal; fingers slightly curved, not meeting when closed. Chela of male larger; fixed finger very short; movable finger abruptly deflexed. Walking legs subequal, order of length 3, 2, 1, 4; 1st pair weakest; dactyls slender, almost straight, equalling propods in length. Abdomen of male tapering gradually, constricted between last two segments, last segment rounded. Abdomen of female smooth, margined with hair.

Color. Ivory yellow faintly tinged with brown.

Dimensions. Female: length of carapace 5.8 mm, width of same 8.2 mm. Male: length of carapace 4.6 mm, width of same 6.2 mm.

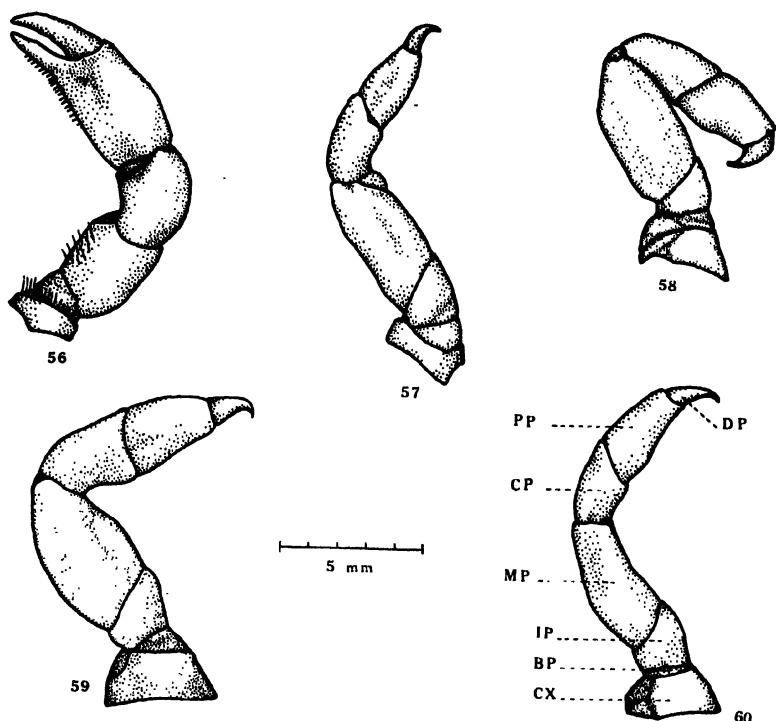
Range. British Columbia to Lower California.

Habitat. Burrows of Upogebia.

Local distribution. Burrows of Upogebia on beach 1.2 miles southeast of Friday Harbor and on Minnesota Reef, San Juan Island; Flat Point, Lopez Island. Reported by Evelyn Way from *Mya arenaria*.

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PINNIXA LITTORALIS, FEMALE

BP - basipodite	IP - ischiopodite
CP - carpopodite	MP - meropodite
CX - coxopodite	PP - propodite
DP - dactylopodite	

- Fig. 56. Right cheliped, dorsal
 Fig. 57. Right first walking leg, ventral
 Fig. 58. Right second walking leg, ventral
 Fig. 59. Right third walking leg, ventral
 Fig. 60. Right fourth walking leg, ventral

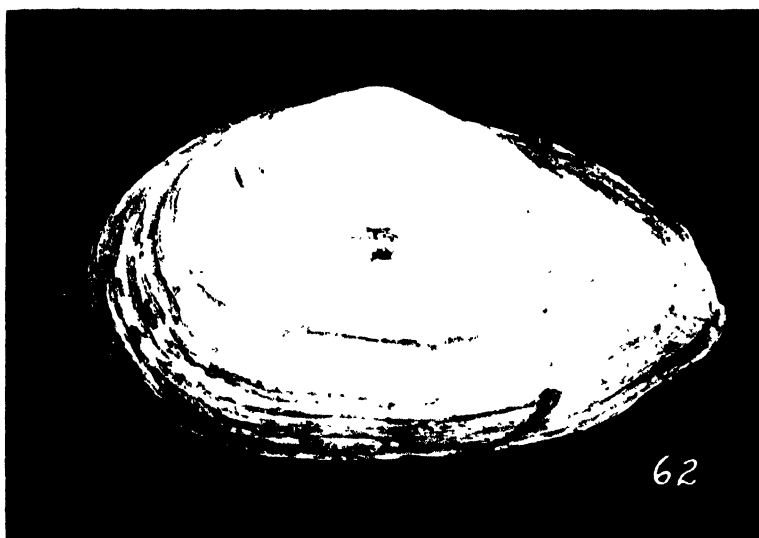


Fig. 61. *Schizothaerus nuttallii*, left valve, $\times .75$

Fig. 62. *Mya arenaria*, left valve, $\times 1$

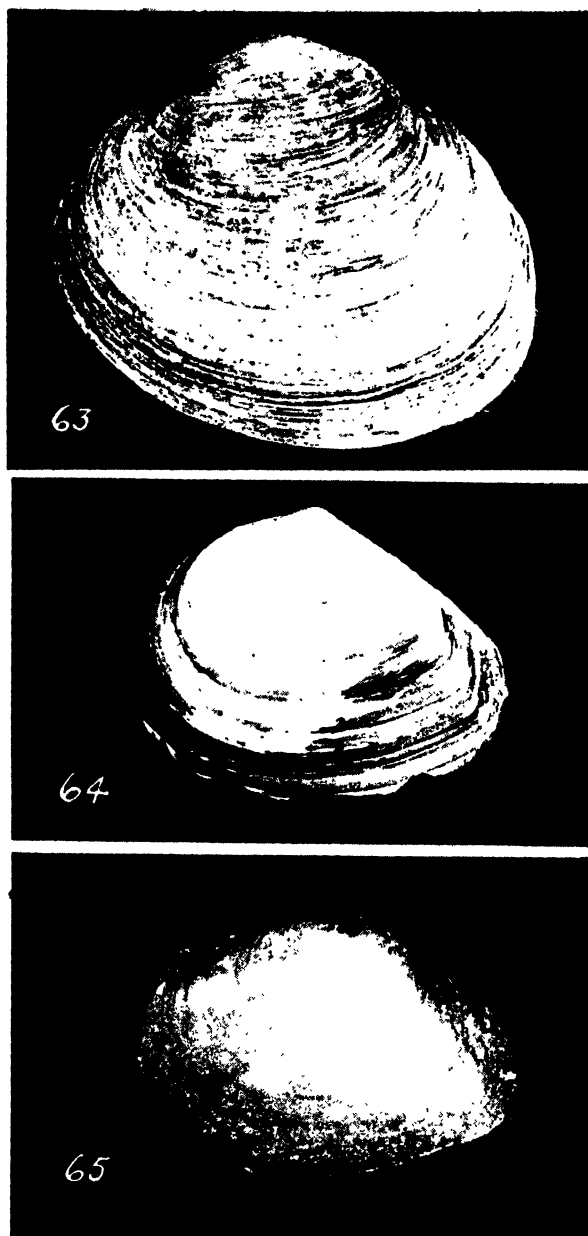


Fig. 63. *Saxodomus giganteus*, left valve, $\times 75$

Fig. 64. *Macoma nasuta*, left valve, $\times 1$

Fig. 65. *Macoma indentata*, left valve, $\times 2.5$

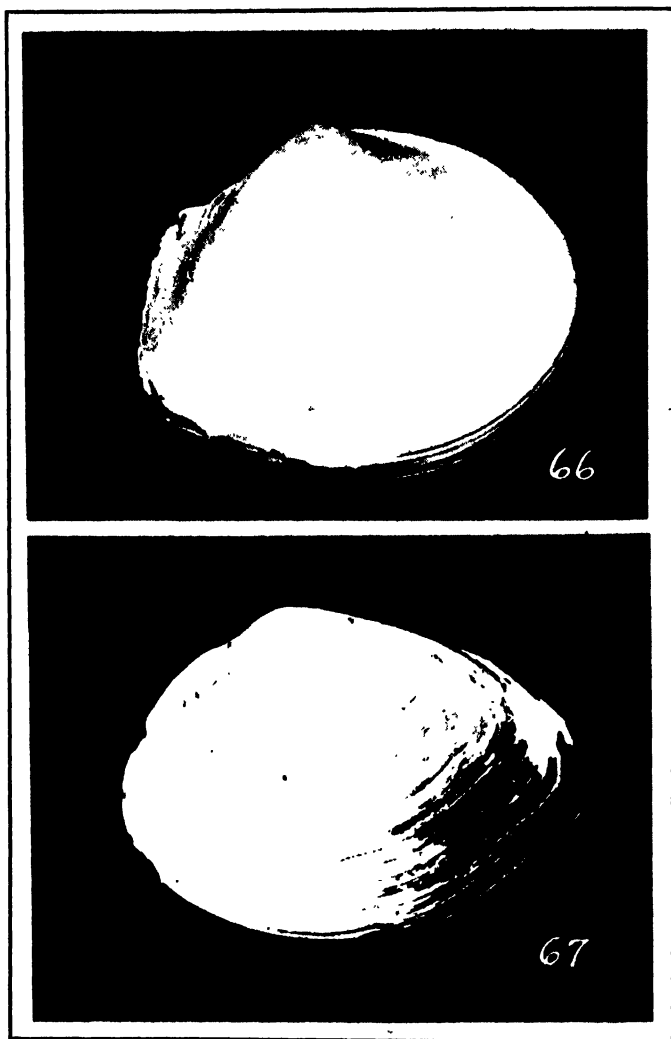


Fig. 66. *Macoma secta*, right valve, $\times 1$

Fig. 67. *Macoma inquinata*, left valve, $\times 1.25$

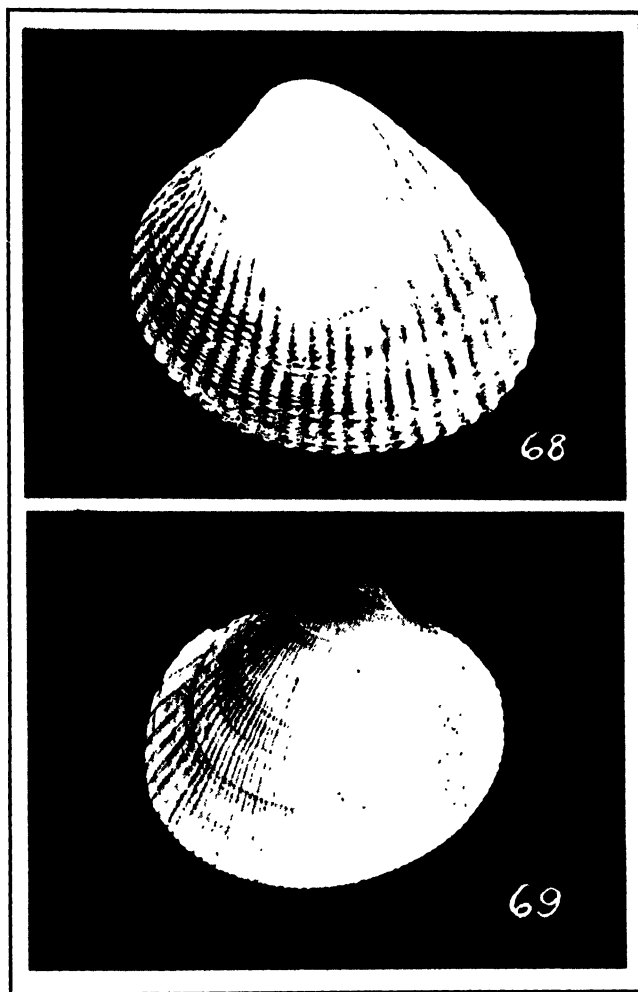


Fig. 68. *Cardium corbis*, left valve, $\times .75$
Fig. 69. *Paphia staminea*, right valve, $\times .75$

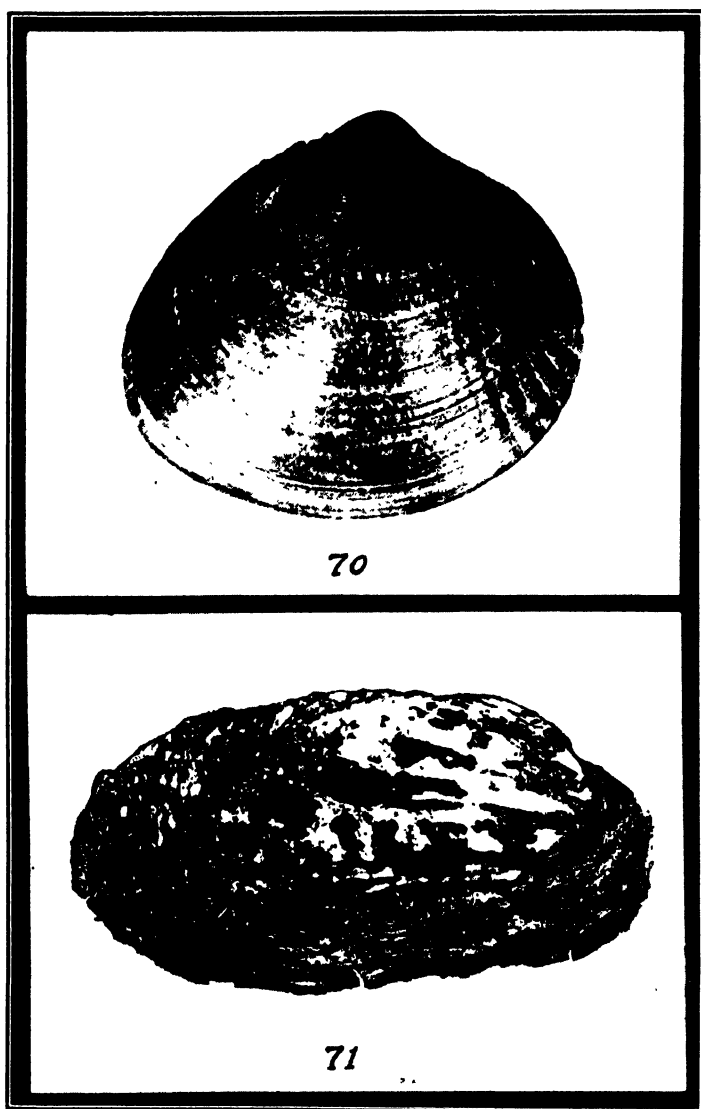


Fig. 70. *Serripes groenlandicus*, left valve, $\times .75$

Fig. 71. *Lyonsia saxicola*, right valve, $\times 1$

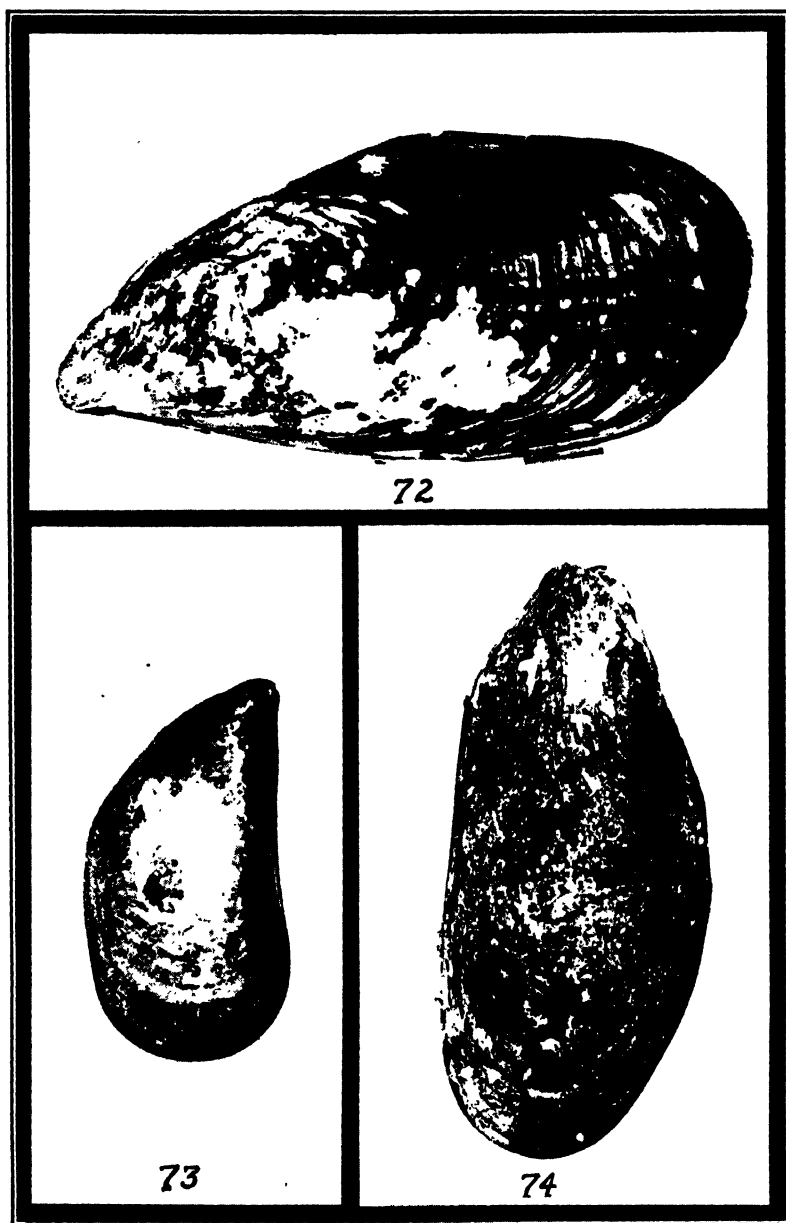


Fig. 72. *Mytilus californicus*, right valve, $\times .75$

Fig. 73. *Mytilus edulis*, left valve, $\times 1$

Fig. 74. *Modiolus modiolus*, right valve, $\times 1$

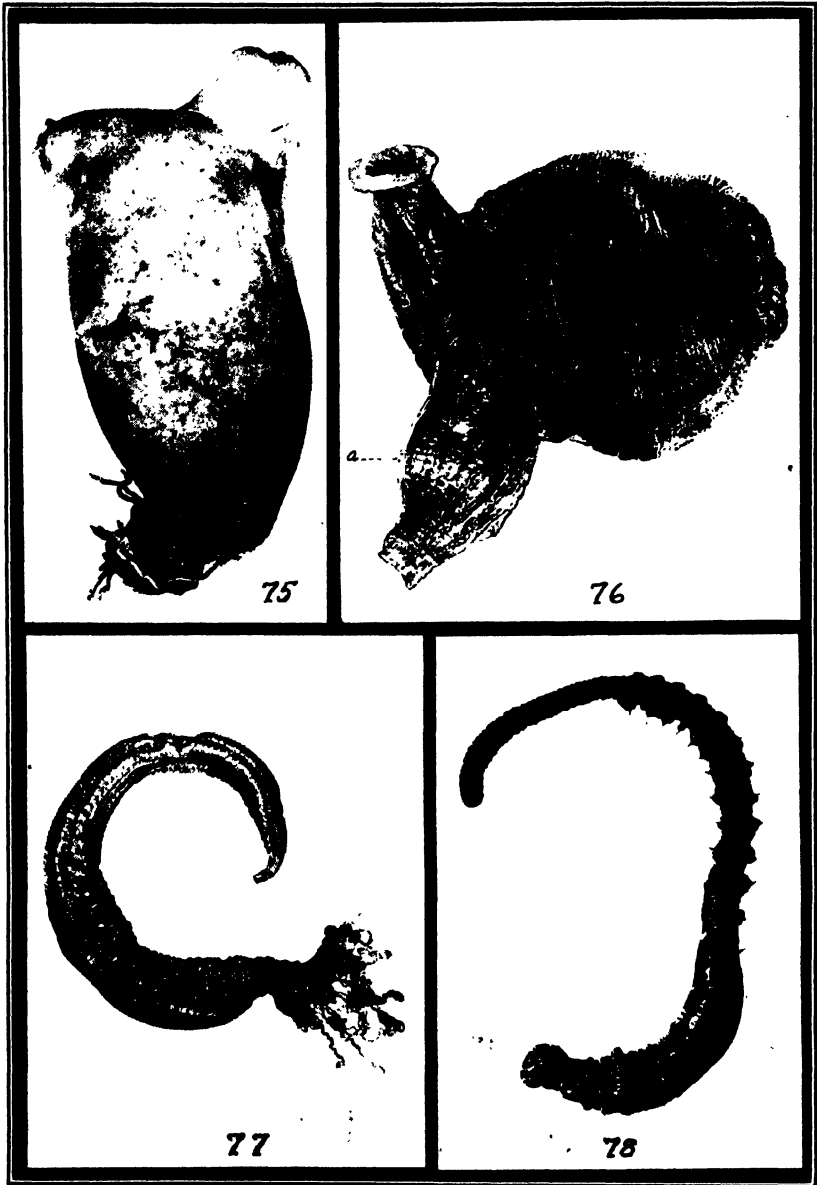


Fig. 75. *Tethyum aurantium*, tunic, $\times 75$

Fig. 76. *Tethyum aurantium*, mantle showing enlargement of atrial cavity (a) caused by *Pinnotheres pugettensis*, $\times 1.5$

Fig. 77. *Amphitrite* sp., $\times 1$

Fig. 78. *Arenicola* sp., $\times 1$

Callianassidae from the West Coast of North America

BELLE A. STEVENS

University of Washington

Received for publication on August 15, 1928.—Editor.

The present paper is based primarily on a large quantity of material collected by the writer in the region about Friday Harbor, and at Sandy Point on Whidby Island, Washington, during the spring and summer of the years 1924-1928. Considerable material from along the coast of British Columbia, Washington, Oregon and California, transmitted to the writer by various persons who have had opportunity to collect it, has been examined and listed for the particular species concerned. The major part of the work was done at the Puget Sound Biological Station, Friday Harbor, Washington.

Professor Trevor Kincaid of the University of Washington has directed the work in general and has contributed much of the information regarding the economic phase. Several oyster growers have also contributed information regarding the relation to the oyster beds. Dr. T. C. Frye, Director of the Puget Sound Biological Station, and Dr. John E. Guberlet of the University of Washington have given many helpful suggestions. Thruout the progress of the work Dr. Waldo L. Schmitt and Dr. Mary J. Rathbun of the Smithsonian Institution have taken a friendly interest and rendered very definite assistance. Mr. S. N. F. Sanford of the Boston Society of Natural History has made available to the writer information concerned in the Journal of the Boston Society of Natural History. To Hallie R. Donaldson, an art instructor in the Seattle Public Schools, is due appreciation for suggestions and aid in retouching the photographs.

The writer is greatly indebted to Mr. Wayne W. Wells of the Southern Oregon Normal School for much of the material collected in the Friday Harbor region and also that from Coos Bay, Oregon. Dr. C. McLean Fraser of the University of British Columbia very kindly permitted the examination of all Callianassidae material in that institution. The material from California was collected by Mr. G. E. MacGinitie of the State Teachers and Junior College, Fresno, California, in connection with an ecological survey at Elkhorn Bay, Monterey, California. The writer wishes to express especial appre-

ciation to these and to the many other individuals and to the classes at the Puget Sound Biological Station who have made possible the collection of so much very inaccessible material, for practically all collection of Callianassidae requires more or less strenuous digging in order to unearth them from their subterranean habitat.

The classification adopted thru the genera is that of Borradaile (Ann. Mag. Nat. Hist. (7) 12:534-551, 1903). Because of the relative obscurity of the group a description of the superfamily, Thalassinidea, has been included in the body of this paper. The color notes are based on live animals.

Practically nothing except a few very general observations has been recorded as to the life history. Little success was attained in the several attempts to rear the larvae. The life history is a problem in itself. Specimens of Upogebia taken at Friday Harbor late in December, 1925, were with eggs. Specimens taken at Allyn, February 3, 1925, were also with eggs. Both Upogebia and Callianassa with eggs have been collected at Friday Harbor thruout the summer but the most are found in this condition in April, May, June and early July.

Two of the greatest difficulties met with are the differentiation of the females in *Callianassa gigas* Stimpson from those in *C. Californiensis* Dana, and the variation in the proportions of the large cheliped of *C. gigas*. In an attempt to clarify these points the writer has measured various parts of numerous specimens and at a later date hopes to publish findings from which more definite conclusions may be drawn. It was decided not to delay the present publication.

Order *Decapoda* Latreille

Suborder *Reptantia* Boas

Tribe ANOMURA Milne-Edwards

Superfamily THALASSINIDEA Ortmann

Body somewhat shrimplike, having the cephalothorax compressed, the abdomen large, symmetrical, elongated and sometimes with well developed pleura, and the appendages of the sixth segment usually adapted for swimming. The carapace and the covering of the abdomen are often more or less membranous. Second to fourth pairs of legs with last joint not curved and flattened. No pleurobranch to the last leg. No transverse suture on telson.

The Thalassinidea are a group of tailed Decapods which resemble the hermit crabs, Paguridea, in some respects and the lobsters and crawfish, Nephropsidea, in others. They are like the Nephrop-

sidea in the shape of the tail-fan and of the first and often also the second leg. They differ from Nephropsidea, as do also Paguridea, in never having the third leg chelate, often in the reduction of the number of gills and in a tendency of the abdomen to become soft and to lose its pleura. This may be connected with their mode of life which is in most cases a burrowing one. In this they show the same habit of concealment as the Paguridea. They are akin to Paguridea also in the thorn-like shape of the antennal scale in such of them as have it well developed, in the freedom of the last thoracic sternite and in their peculiar way of carrying the last pair of legs rather apart from and above the rest. They differ from the hermit crabs in that these legs are shaped much like the rest, that their second pair of legs is usually chelate, and that their abdomen is symmetrical with a broad tail-fan. A remarkable feature, which recalls the prawns, is the presence in most of them of a special process of the endopodite known as the appendix interna on the abdominal limbs.

The superfamily, Thalassinidea, comprises 4 families of which Axiidae and Callianassidae are represented on the Pacific Coast of North America. The present paper is concerned with the representatives of Callianassidae only.

KEY TO THE FAMILIES OF THE THALASSINIDEA

(The present paper is concerned with Callianassidae only.)

- A. No linea thalassinica; both movable and fixed antennal thorns present, tho sometimes minute (questionably absent in *Scytoleptus*); abdominal pleura large. *Axiidae*
- AA. Linea thalassinica present (except in Callianidea); fixed antennal thorn wanting, scale reduced to a flattened vestige or wanting; abdominal pleura usually small.
 - B. Sutures on both exopodite and endopodite of last limb; abdominal pleura of a good size. *Laomediidae*
 - BB. No sutures on the last limb; abdominal pleura small.
 - C. Second leg chelate or simple; no podobranchs on legs. 3rd-6th abdominal limbs broad; with vestige of antennal scale. *Callianassidae*, p. 318
 - CC. Second leg subchelate; podobranchs on first three legs; abdominal limbs all narrow; without vestige of antennal scale. *Thalassinidae*

Family *Callianassidae* Bate

Body shrimp-like. Rostrum may be either of a good size or small. Linea thalassinica present. Antennal peduncle 5 jointed; antennular flagella short or of moderate length; antennal scale quite vestigial; no antennal thorn. Abdomen extended; abdominal pleura small or absent. Tail-fan well developed and adapted for swimming. First pair of legs unequal or subequal, usually chelate or subchelate but sometimes simple, second pair chelate or simple, third and fourth pairs simple, others variable; legs without podobranchs and usually without mastigobranchs, without pleurobranch. Gills trichobranch or with filaments broadened in various degrees. Third to fifth abdominal limbs with or without appendix interna, their branches broad, and the last pair of limbs without suture on endopodite or exopodite.

Of 13 genera, 2 are represented on the west coast of North America.

KEY TO THE GENERA OF CALLIANASSIDAE FROM THE WEST
COAST OF NORTH AMERICA

- A. Rostrum of good size tho short; first pair of legs alike and subequal. Eye peduncles cylindrical; external maxillipeds pediform. *Upogebia*, p. 318
- AA. Rostrum small, rudimentary or absent; first pair of legs not alike and very unequal; eye peduncles flattened; external maxillipeds operculiform. *Callianassa*, p. 324

Genus *Upogebia* Leach

Rostrum of good size tho short, tridentate, rough and hairy. First pair of legs alike and subequal, with very small pollex, chelate or subchelate; second, third and fourth pairs not chelate, fifth pair usually not chelate. First pair of pleopods different from the following 4 pairs. No appendix interna on abdominal limbs 3-5. Eye peduncles cylindrical, cornea terminal. External maxillipeds pediform.

Upogebia pugettensis (Dana). Figs. 1-5, 20-37.

Gebia pugettensis Dana, Proc. Acad. Sci. Phila. 6:19, 1852; and Crustacea, U.S. Expl. Exped. 1:510, 1852, pl. 32, fig. 1, 1855; Stimpson, Jour. Boston Soc. Nat. Hist. 6:488, pl. 21, fig. 2, 1857; Lockington, Ann. Mag. Nat. Hist. (5), 2:299, 1878.

Gebia californica Stimpson, Proc. Calif. Acad. Sci. 1:88, 1856.

Upogebia pugettensis Holmes, Occas. Papers Calif. Acad. Sci. 7:157, 1900; Rathbun, H. A. E. 10:153, 1904; Schmitt, Univ. of Calif. Pub. in Zool. 23:115, fig. 77, 1921.

Characters. Upper portion of carapace in front of cervical groove flattened, scabrous, hairy and marked with three longitudinal grooves, median groove the shortest; front tridentate, with median

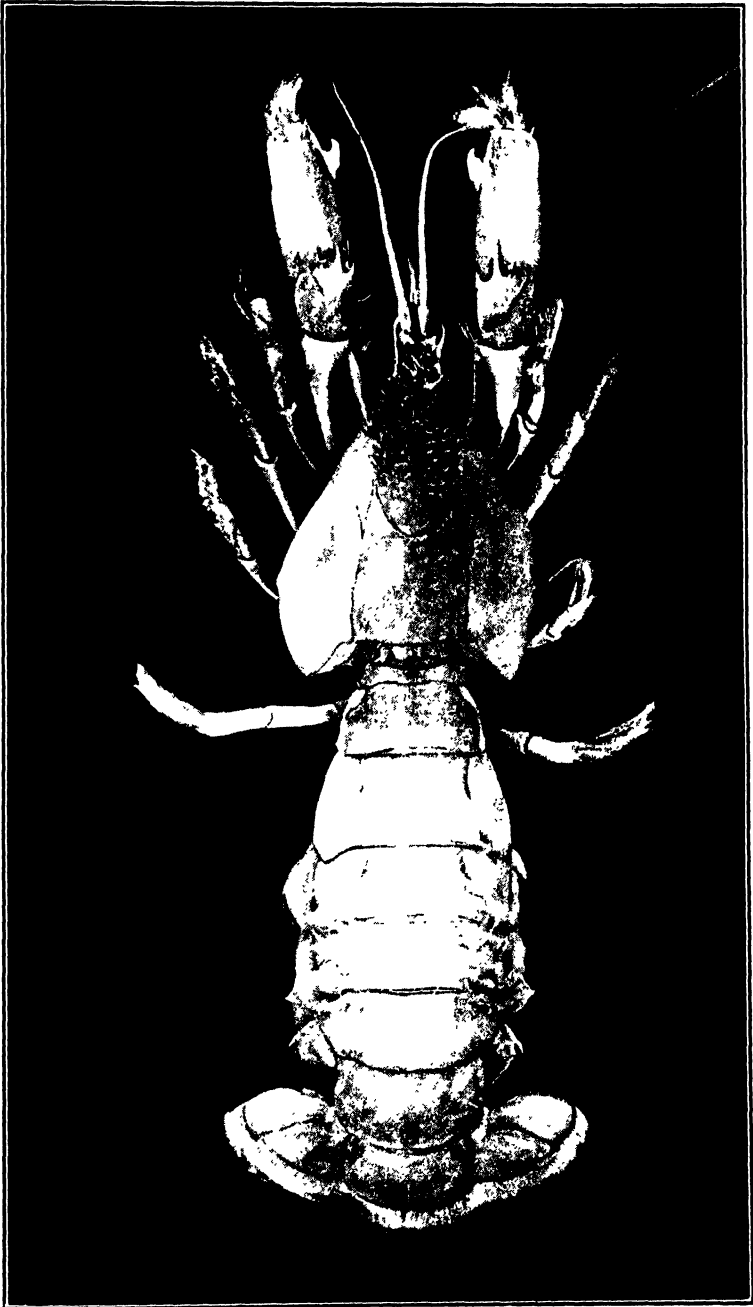


Fig. 1. *Upogebia pugettensis* (Dana) male, dorsal. $\times 1$.

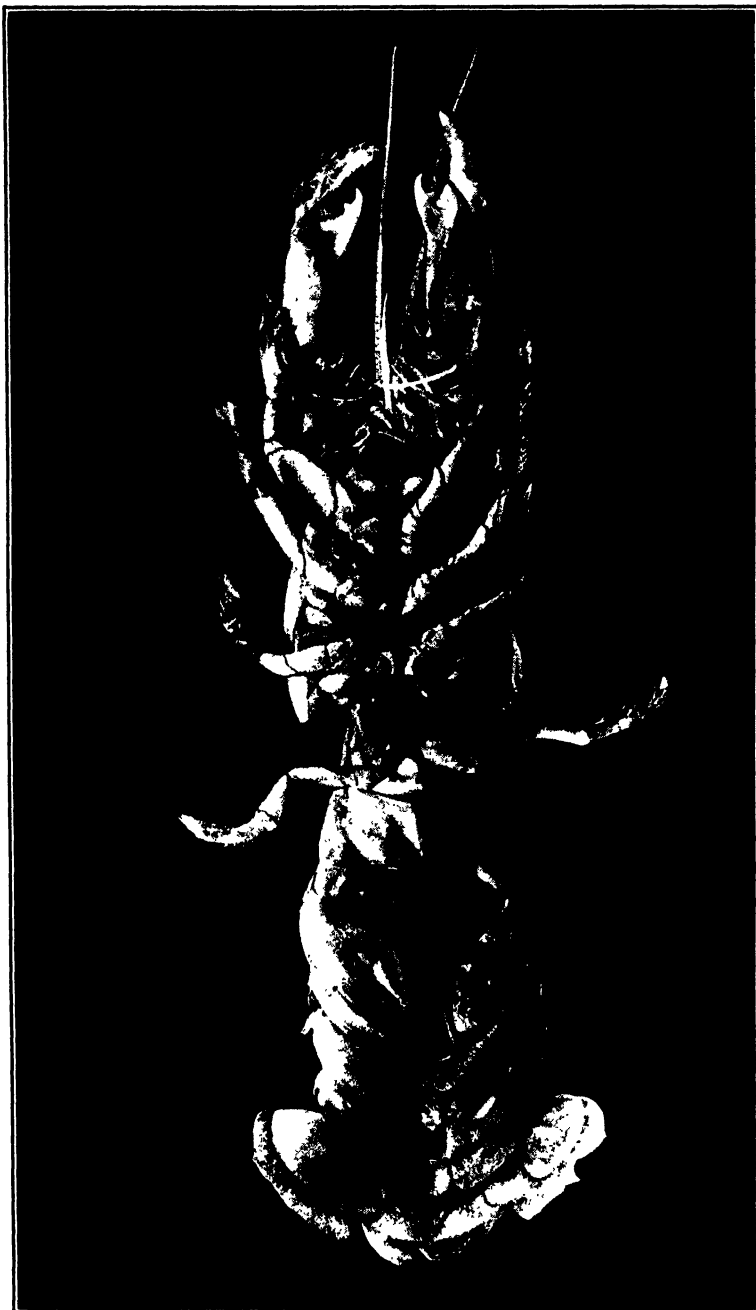


Fig. 2. *Upogebia pugettensis* (Dana) male, ventral. $\times 1$.

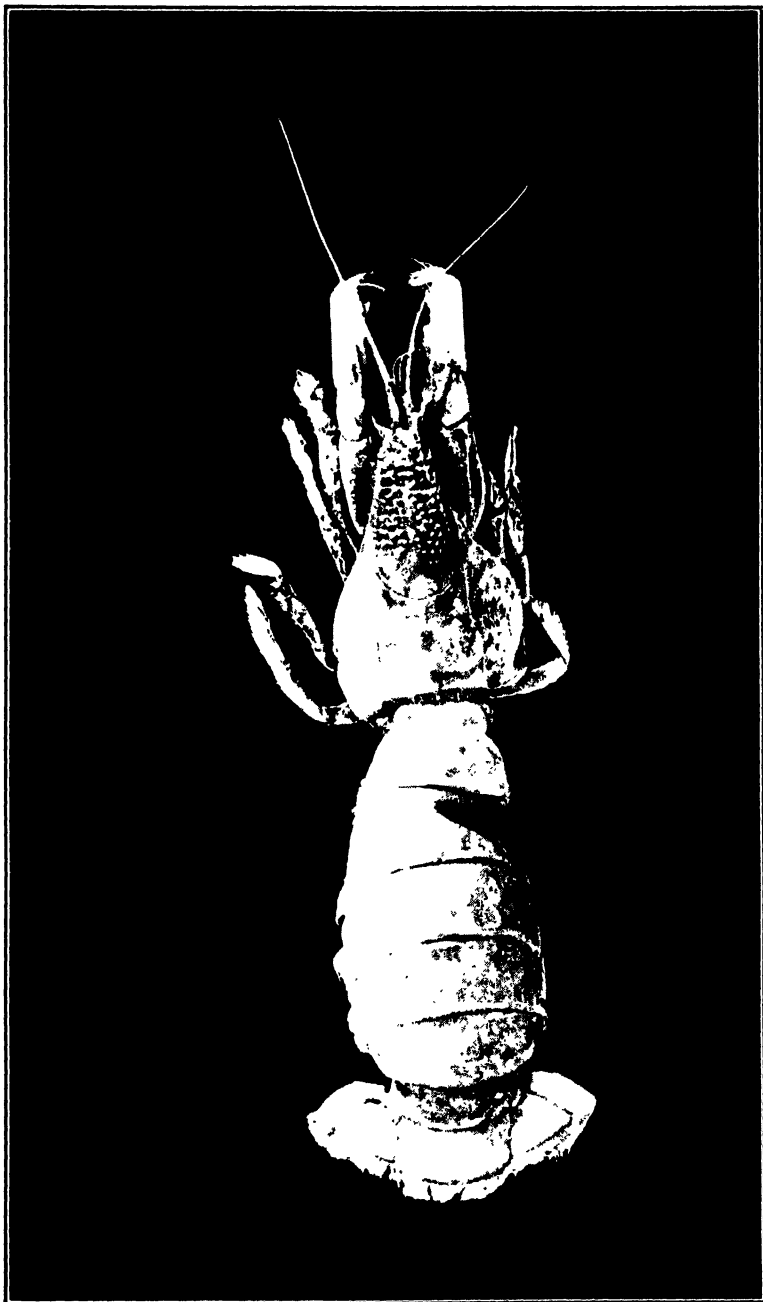


Fig. 3. *Upogebia pugettensis* (Dana) female, dorsal. $\times 1$.

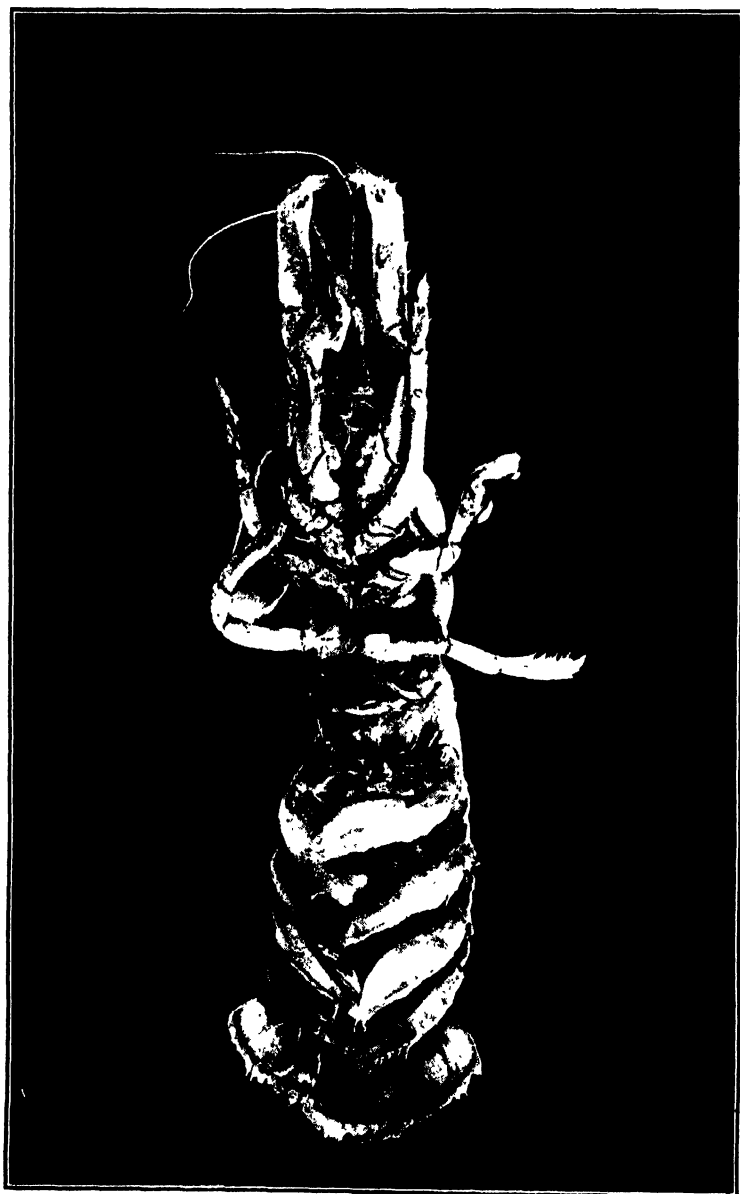


Fig. 4. *Upogebia pugettensis* (Dana) female, ventral. $\times 1$.

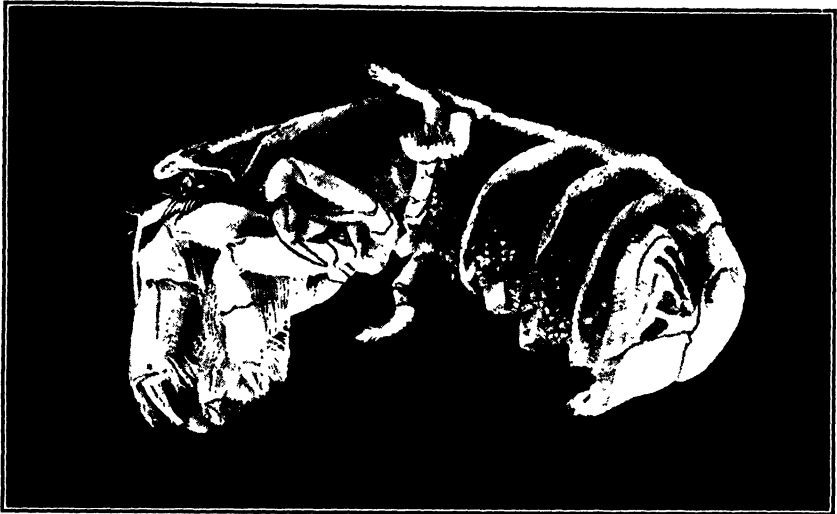


Fig. 5. *Upogebia pugettensis* (Dana) female, with eggs. $\times 1$.

tooth large, horizontal and triangular, lateral teeth short. A minute marginal spine generally present a short distance below the lateral teeth. Eye-stalks short, reaching very little farther forward than lateral teeth of front. Antennule less than half the length of the antenna, flagella subequal. Peduncle of antenna exceeds that of antennule; flagellum ciliate and longer than carapace. Chelipeds equal; merus spinulose and hairy below; carpus with upper and lower edges spinulose and having a spine at the antero-internal angle and another spine a short distance below it; hand with two parallel, scabrous, hairy lines on the upper edge, a transverse granulated line at the proximal end of the inner surface and a line of hairs on the outer surface which is continued obliquely across the carpus; lower side of palm scabrous and hairy; pollex short, bent downward but with the tip turned upward and having a posteriorly directed tooth near middle; dactyl obliquely compressed, incurved, acute, projecting, when closed far beyond the tip of the pollex. Ambulatory legs stout, ciliate; first, second and third somewhat compressed, fourth very little compressed; first and second subequal and longer than the third and fourth which are subequal; first pair considerably longer than the carapace. Uropods short, the inner ramus distally rounded, truncate, the outer rounded. Telson entire, rectangular, wider than long.

Dimensions. Type: length 50.8 mm.

Color. The younger specimens are vinaceous-buff, densely mottled with deep olive to king's blue above, while in the older specimens the

mottling is deep olive; tips of chelipeds and spines light ocraceous-buff; hair muddy tan. In specimens kept in a live box for a few days the deep olive is entirely replaced by king's blue which may appear even on the chelipeds and walking legs.

Type locality. Puget Sound.

Distribution. From Southern Alaska to San Quentin Bay, Lower California (Lockington).

Specimens have been examined by the author from the following locations: *British Columbia*: off Lasqueti Island, at 30-50 meters (tide not known); Locke Bay; Roberts Bay near Sidney, Port Renfrew, Tofino Inlet, Vancouver Island (in the collection at the University of British Columbia); *Washington*: Fossil Bay, Sucia Island; East Sound, Orcas Island; Samish; Blakely Island; Brown Island; beach at Jensen's shipyard a little southeast of Friday Harbor, Minnesota Reef, Argyle, False Bay, Kanaka Bay, Smallpox Bay on San Juan Island; Davis Bay and Flat Point on Lopez Island; Poulsbo; Sea-beck; Tracyton; Des Moines; Allyn; Oyster Bay; *Oregon*: Coos Bay.

Localities worthy of note represented in the U.S. National Museum are: *Southeastern Alaska*: Kasaan Bay, Prince of Wales Island; Union Bay, Cleveland Peninsula; Thorn Arm; *British Columbia*: Nanaimo; Comox; Departure Bay; Otter Bay; Pender Island; *Washington*: Sucia Island; *California*: mouth of the Tia Juana River, San Diego County (Rathbun).

Remarks. The tooth of the pollex is sometimes absent, as it was in the specimen described by Dana. "This tooth," says Stimpson, "is a prominent character in all the very numerous specimens in the Smithsonian Museum, but it is obsolete in the specimen described by Dana, altho actual comparison shows them to be the same." In some small specimens from Catalina Island the small marginal spine beneath the lateral teeth of the front was absent, altho they agreed with specimens from northern California in every other essential feature (Holmes).

Genus *Callianassa* Leach

Rostrum short, triangular, rudimentary or absent. First pair of legs dissimilar and very unequal, with well developed chelae; second pair small and chelate, third and fourth pairs simple, fifth pair subchelate. First two pairs of pleopods different from the following three pairs. An appendix interna on abdominal limbs 3-5. Eye-stalks flattened, cornea dorsal and median, small or absent. External maxillipeds operculiform.

KEY TO THE SPECIES OF *CALLIANASSA* FROM THE WEST
COAST OF NORTH AMERICA

- A. Front with median tooth either obscure or not prominent; eyes pigmented.
 - B. Eye-stalks acute, their inner extremities not tuberculiform, divergent or not; cornea at about middle of stalk.
 - C. Hand of first ambulatory leg with pollex about 1.5-2 times as broad at base as dactyl; lobe at infero-proximal angle of merus of large cheliped not covered when carpus is bent at right angles to merus; extremities of eye-stalks divergent. *C. gigas*, p. 325
 - CC. Hand of first ambulatory leg with pollex and dactyl subequal at base or the pollex slightly broader; lobe at infero-proximal angle of merus of large cheliped almost completely covered when carpus is bent at right angles to the merus; extremities of eye-stalks usually divergent. *C. californiensis*, p. 333
 - BB. Eye-stalks with their inner extremities tuberculiform and not divergent; cornea considerably in front of middle of eye-stalk. *C. affinis*, p. 341
- AA. Front with sharp and prominent median tooth; eyes not pigmented. *C. goniophthalma*, p. 342

Callianassa gigas Dana. Figs. 6-9, 14 15, 38-54.

Callianassa gigas Dana, Proc. Acad. Nat. Sci. Phila. 6:19, 1852; Crust. U.S. Expl. Exped. 1:512, 1852, pl. 32, fig. 3, 1855; Stimpson, Jour. Boston Soc. Nat. Hist. 6:489, pl. 21, fig. 3, 1857; Milne-Edwards, A., Nouv. Archiv. Hist. Nat. Paris 6:81, 1870; Lockington, Ann. Nat. Hist. (5), 2:302, 1878; Holmes, Occas. Papers Calif. Acad. Sci. 7:162, 1900; Rathbun, H. A. E. 10:154, 1904; Schmitt, Univ. of Calif. Publ. in Zool. 23:119, fig. 80, 1921.

Callianassa longimana Stimpson, Proc. Boston Soc. Nat. Hist. 6:86, 1857; Jour. Boston Soc. Nat. Hist. 6:490, pl. 21, fig. 5, 1857; Cooper, Rep. Expl. and Sur. to Pacific Ocean 12: book 2, 388, 1860; Bate, in Lord's Nat. in Vancouver's Is. 2:270, 1866; Challenger Reports 24:19, 1888; Milne-Edwards, A., Nouv. Archiv. Hist. Nat. Paris 6:83, 1870; Lockington, Ann. Nat. Hist. (5) 2:302, 1878; Holmes, Occas. Papers Calif. Acad. Sci. 7:161, pl. 2, fig. 28, 1900; Rathbun, H. A. E. 10:154, 1904; Hilton, Jour. Ent. Zool. Pomona Coll. 8:63, fig. 14, 1916; Schmitt, Univ. of Calif. Publ. in Zool. 23:117, fig. 79, 1921.

Characters. Median tooth of front small but subacute, with two small lateral teeth as in *C. californiensis*. Eye-stalks similar to those in preceding species but with sides subparallel to about the middle, beyond which the outer margin turns inward more or less abruptly

and continues in a straight or somewhat incurved line; inner margins of the two approximated from the base to about two-thirds the length where they diverge, each to meet the outer margin of the corresponding stalk forming an acute tip which may be somewhat upturned; pigmented cornea at about the middle or just behind the middle of the stalk. Antennules much as in the preceding species. Antennae about one-half as long as the body. Chelipeds in the adult male very unequal, narrower than in *californiensis*; outer surface smooth and glossy except on ischium, margins more or less ciliate and minutely serrulate or denticulate. Large cheliped (adult male) with ischium of similar shape to that of *californiensis* but with the inner surface granulated and the outer surface more or less scabrous; merus similar to that of *californiensis* but the upper margin is not curved and the lobe at the base is more prominent; carpus about three-fourths as wide as long, little longer than merus, usually subequal to palm (may vary greatly), with outer surface very convex, margins subparallel, ciliate, minutely serrulate, thin but slightly produced, the posterior margin below the articulation of the merus very slightly produced backwards into a broadly and evenly rounded lobe; hand the same width and longer than the carpus, strongly compressed but somewhat convex both above and below; palm longer than broad, usually about as long as carpus, with thin, ciliate, parallel margins; practically no hiatus between fingers when closed; small upturned tooth between bases of fingers; fingers shorter than palm and furnished with tufts of hair; pollex bent upward near the tip, upper surface denticulate; dactyl slightly longer than pollex, hooked at tip; upper and lower margins denticulate, inner surface more or less granulated, in adult individuals the prehensile margins of the fingers may be practically without teeth. Small cheliped (male) resembles that of *californiensis* but the carpus is relatively longer and narrower. Large cheliped in the female scarcely distinguishable from that of the female of *californiensis* except that the lobe at the infero-proximal angle is little more than a sharp spine while in *californiensis* it takes more nearly the form of that in the adult male (young males of both species have a small spine). Small chelipeds (female) are also very similar in the two species but in *gigas* the hand and carpus are often somewhat longer and narrower. This difference is not constant even in adult specimens. In both male and female the lobe at the infero-proximal angle of the merus of the large cheliped is not covered when the carpus is bent at right angles to the merus. Ambulatory legs very similar to those in *californiensis* except the first which has the hand with lower margin very convex but becoming slightly concave near

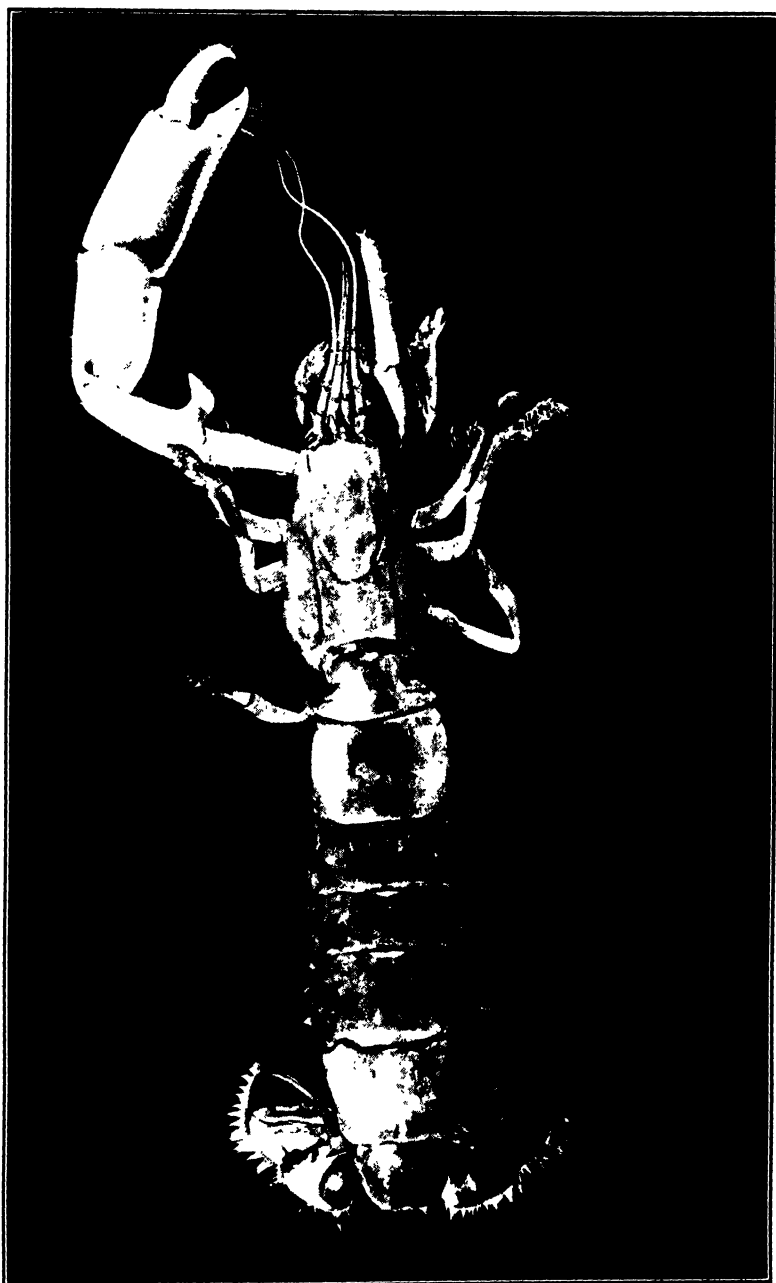


Fig. 6. *Callianassa gigas* Dana, male, dorsal. $\times 1$.



Fig. 7. *Callinassa gigas* Dana, male, ventral. $\times 1$.

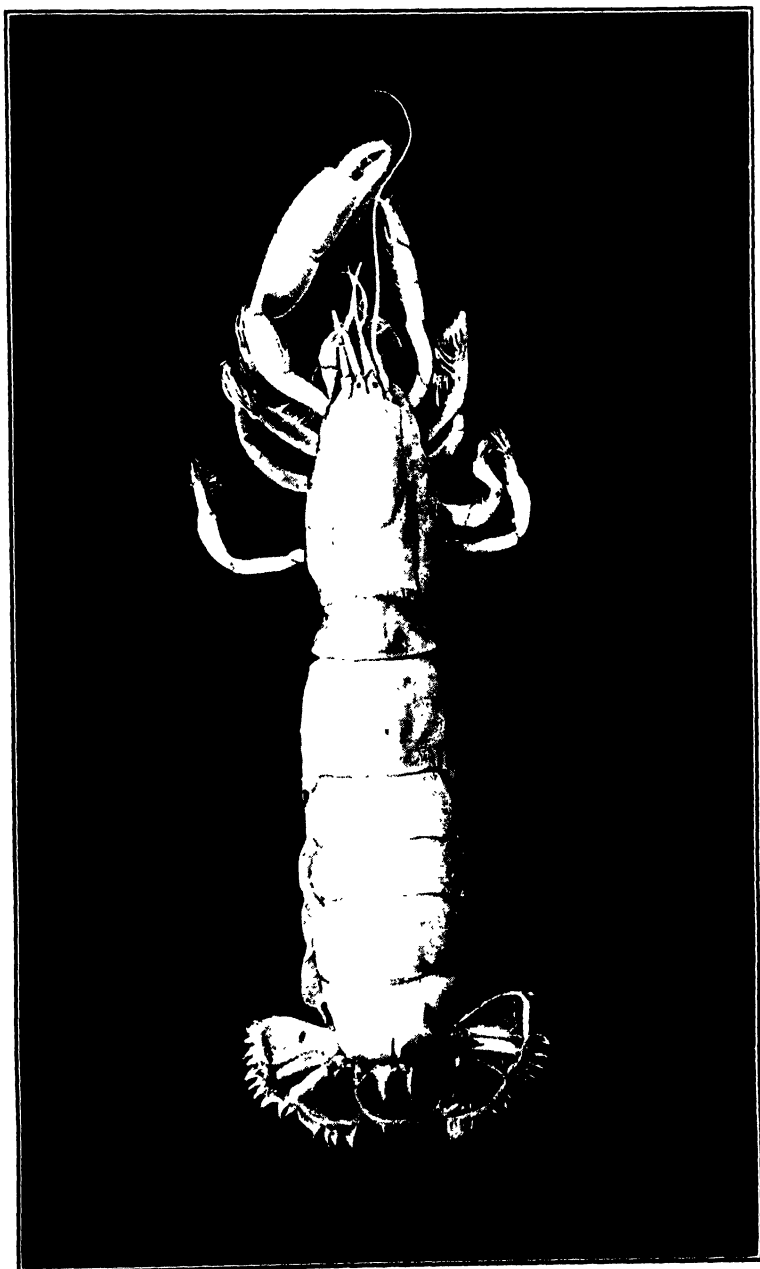


Fig. 8. *Callianassa gigas* Dana, female, dorsal. $\times 1$.

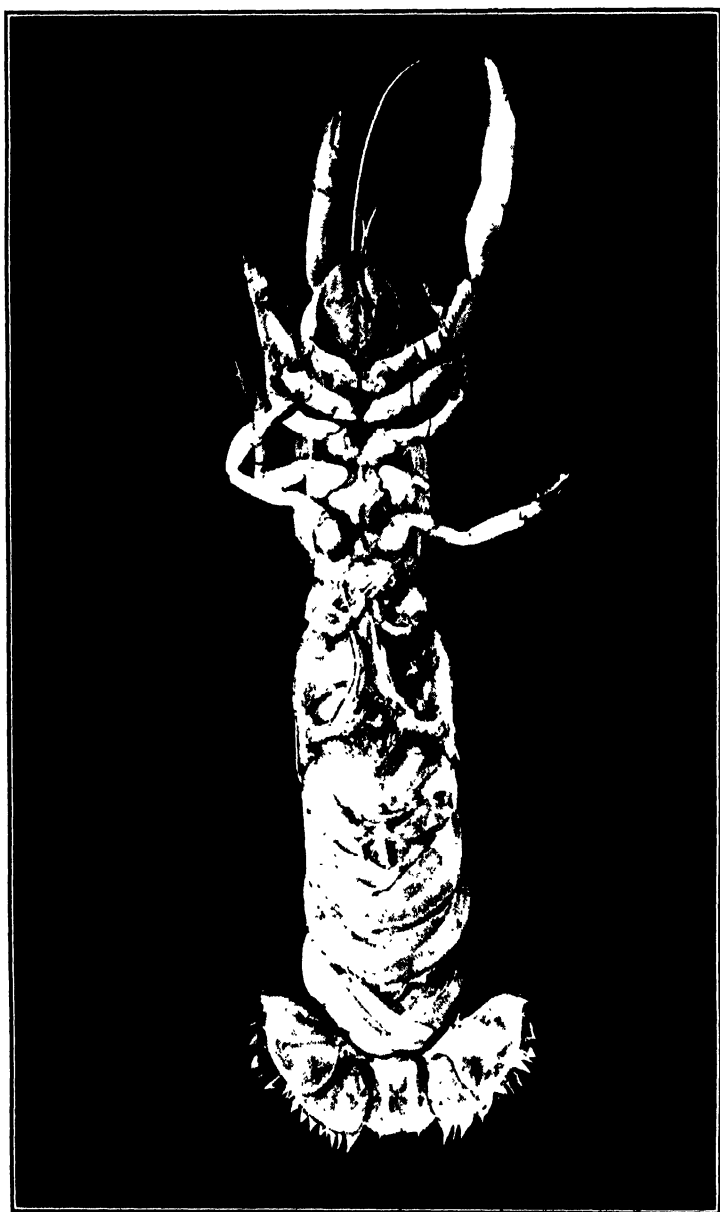


Fig. 9. *Callianassa gigas* Dana, female, ventral. $\times 1$.

the tip of pollex, the pollex about one and a half to two times as broad at base as the dactyl. Telson and uropods much as in *californiensis*.

Dimensions. Of type: length 114 mm.

Color. Usually white to cream; body may be pinkish orange to pink or orange or white; chelipeds white; leaf-like pleopods may be orange.

Type locality. Puget Sound.

Distribution. From Vancouver Island, British Columbia (Bate); to San Quentin Bay, Lower California (Lockington); Puget Sound (Dana, Calman); Gulf of the Farallones, California, 39 meters ("Albatross" station 3150), one fragmentary specimen showing the large cheliped and portion of abdomen (Rathbun). G. E. MacGinitie has reported to the author one male and one female from Elkhorn Slough, Monterey Bay, California.

Specimens have been examined by the author from the following locations: *British Columbia*: Boundary Bay (in the collection at the University of British Columbia); *Washington*: Fossil Bay, Sucia Island; Brown Island; beach at Jensen's shipyard southeast of Friday Harbor, False Bay, San Juan Island; Poulsbo; Allyn (about 150 meters south of wharf).

Remarks. Puget Sound has been cited by preceding writers as the type locality for *Callianassa gigas* Dana. At the close of the second summer's collection after having examined hundreds of *Callianassa* from various locations along Puget Sound, no specimen could be assigned definitely to *gigas*. According to Schmitt (Univ. of Calif. Publ. in Zool. 23:117-119, 1921) *Callianassa longimana* Stimpson has the "median tooth of front small and subacute" while *gigas* has the "front with a sharp median tooth." This character of *gigas* appears in the drawing of the whole animal by Dana (Crustacea, U.S. Expl. Exped. pt. 1, pl. 32, figs. 3, 3c, 1852) but in the description Dana (Proc. Acad. Nat. Sci. Phila. 6:19, 1852) gives it "*Frons paulo triangulatus*" (Front somewhat triangular). In other respects the two species are described by all writers concerned as similar except in the relative proportions of the carpus of the large cheliped which has proved to be an exceedingly variable characteristic. Accordingly a large series containing many variations was assigned to *longimana* and representatives sent to Dr. Waldo L. Schmitt of the Smithsonian Institution, U.S. National Museum, who verified the determination. However, as the series was enlarged and data accumulated it became apparent that the two species merge into one another and are in reality identical.

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Following are the results of investigation of the literature concerned and also of correspondence in an effort to locate specimens which the earlier workers had designated as *gigas*. Dana's figure of the whole animal shows the large cheliped turned so that the merus is "broadest at the distal end." This is a characteristic of *gigas* according to Kingsley ("Key to the Astracoid and Thallinoid Crustacea of the U.S.," Amer. Nat. 33:823-824, figs. 2, 3, 1899). In a more detailed drawing by Dana (fig. 3c) the merus is somewhat "tapering towards the distal extremity," which is a characteristic of *longimana* according to Kingsley. The tooth at the base of the merus of Dana's figure of *gigas* is small but that is usual in females and in young males. Dana does not state whether the specimen figured is male or female and nothing is stated as to the magnification of the drawing. Dr. J. S. Kingsley of the University of Illinois was consulted with regard to the diagnostic characteristics concerned in his key and he offered no objection to proposed changes in classification. The figure in Stimpson (Jour. Boston Soc. Nat. Hist. 6:489, pl. 21, fig. 3, 1857) appears to be an exact reproduction of the large cheliped from the drawing of the whole animal by Dana, and the one by Kingsley to be the same drawing reduced. Kingsley states "meros long, broadest at the distal end;" Dana says of the distal end of the merus "sed vix latiore" (but scarcely broader). Holmes (Occas. Papers Calif. Acad. Sci. 7:162, 1900) and succeeding writers omit this point entirely but the confusion in interpretation of the description still exists. Dr. J. S. Holmes of the University of California has written that so far as he can discover there are no specimens of *gigas* in the collection there and adds that in his synopsis he simply transcribed Dana's description. H. A. Pilsbury, curator at Phila. Acad. Nat. Sci., states that the type specimen of *gigas* is probably no longer extant. The only other reference not cited in the synonymy for this species from this part of the world is Calman ("On a Collection of Crustacea from Puget Sound," Ann. N.Y. Acad. Sci. 11(13):260, 1898) in which he merely lists it. At Dr. Schmitt's suggestion an inquiry was sent to Dr. W. T. Calman of the British Museum of Natural History who arranged with Professor A. D. Peacock of the Museum at University College, Dundee, for the loan of a specimen labeled "*C. gigas*, Puget Sound." This specimen was collected by Dr. Calman about 30 years ago. This specimen is a female practically identical with one of the large *longimana* in the present collection. Dr. Schmitt states that the identification of the specimen labeled *gigas* at the U.S. National Museum is doubtful. This specimen is a badly damaged female of which the frontal margin is lacking. Consequently the

identification by Dr. Mary J. Rathbun of the U.S. National Museum was necessarily made on the basis of the chelipeds, there being no other characteristic parts present.

As a result of the investigation summarized above it seems that either *gigas* has not been taken since Dana's specimen or that the species *gigas* and *longimana* are virtually one. In the light of the evidence presented, the latter, in the opinion of the writer, is the more logical conclusion. The confusion existing in classification may very easily have arisen and persisted in the literature thru not having sufficiently large series of specimens, probably due to the difficulty in collecting. It seems possible that the younger males were formerly assigned to *gigas*, the older males to *longimana*, and the females to either species. The fact that in the adult females the large chelipeds are quite different from those in the adult males but similar to those in the young males may have added to the general difficulty. The various *longimana* reported are probably just mature *gigas*. There is nothing in the original description of *gigas* to exclude *longimana* from that species except the relative proportions of the carpus of the large cheliped which is found to be a variable characteristic. In both species the proportions are fairly constant in the females and in the young males, but in the older males there are decided variations which do not appear even in the medium sized specimens. It is now proposed that *Callianassa longimana* Stimpson revert to the older species, *Callianassa gigas* Dana. The definition of *gigas* is accordingly amended.

Callianassa californiensis Dana. Figs. 10-13, 16-17, 55-71.

Callianassa californiensis Dana, Proc. Acad. Nat. Sci. Phila. 7:175, 1854; Stimpson, Jour. Boston Soc. Nat. Hist. 6:489, pl. 21, fig. 4, 1857; Milne-Edwards, A., Nouv. Archiv. Hist. Nat. Paris 6:82, 1870; Lockington, Ann. Nat. Hist. (5) 2:301, 1878; Holmes, Occas. Papers Calif. Acad. Sci. 7:159, pl. 2, fig. 27, 1900; Rathbun, H. A. E. 10:154, 1904; Hilton, Jour. Ent. Zool. Pomona Coll. 8:63, 1916; Schmitt, Univ. of Calif. Pub. in Zool. 23:117, fig. 78, 1921. *Callianassa occidentalis* Stimpson, Proc. Calif. Acad. Sci. 1:88, 1856.

Characters. Median tooth of front very short and rounded, with a small triangular tooth on either side between bases of ocular peduncles and antennae. Eye-stalks variable, reaching a little beyond the end of the first antennular segment, about twice as long as wide, sides usually subparallel for less than half the length, beyond which the outer margin continues on a fairly even curve to the tip; inner margins approximated the entire length or from the base to about two-thirds the length, at which point they diverge more or less abruptly, either continuing in a straight line or incurving to

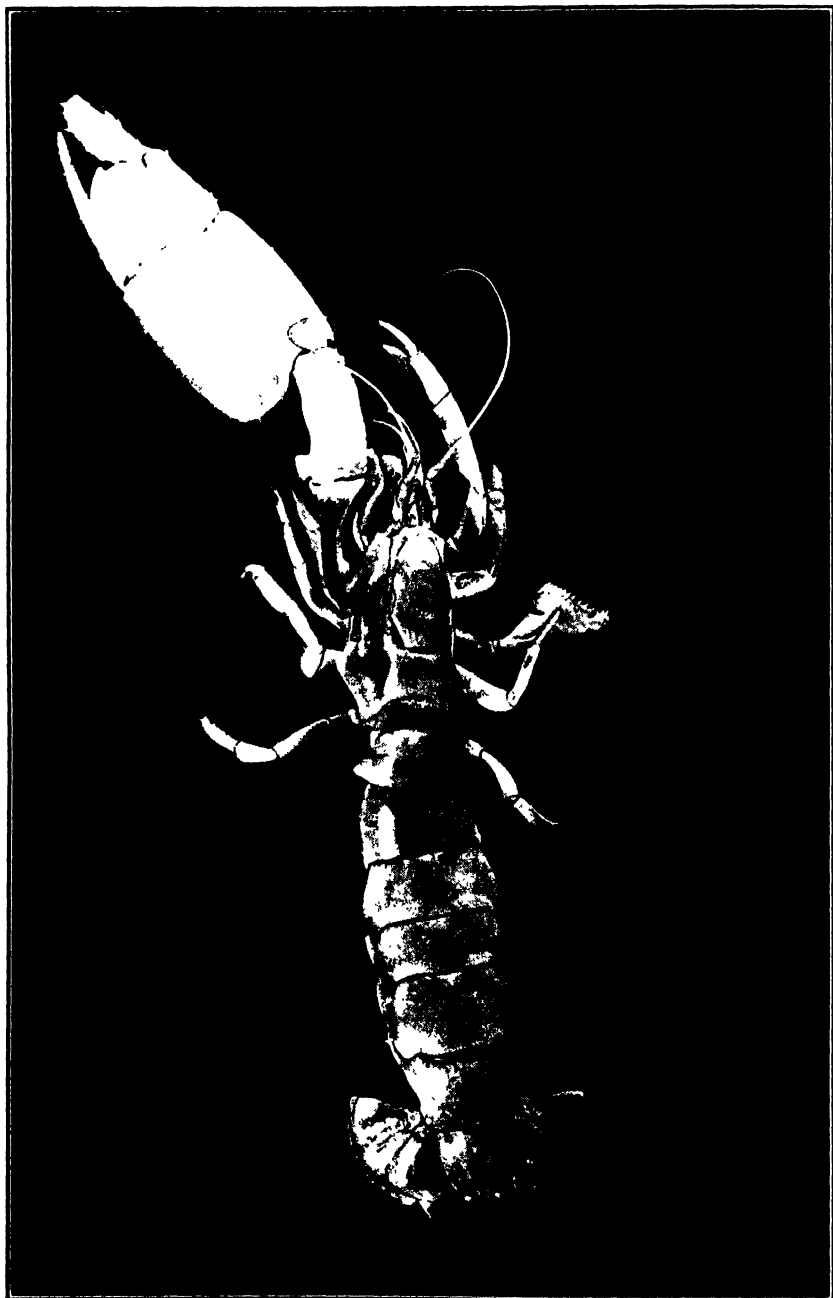


Fig. 10. *Callinassa californiensis* Dana, male, dorsal. $\times 1$.



Fig. 11. *Callianassa californiensis* Dana, male, ventral. $\times 1$.



Fig. 12. *Callinassa californiensis* Dana, female, dorsal. $\times 1$.



Fig. 13. *Callinassa californiensis* Dana, female, ventral, with eggs. $\times 1$.

form a prominent angle; tips acute, may be upturned; pigmented cornea at about the middle of the stalk. Antennule about one-third the length of the antenna, flagella subequal. Antennae from one-half to two-thirds the length of body, peduncle nearly equal in length to that of the antennules. Chelipeds in adult male very unequal, either the right or the left enormously developed; inner and outer surfaces smooth and glossy, margins more or less ciliate and minutely serrulate or denticulate except the upper margin of the ischium. Large cheliped (adult male) with ischium slender, compressed, incurved, distally widened, and finely denticulate on acute,

lower margin; merus about as long as ischium (generally a little longer) but stout, curved, almost naked except on ciliate margins, furnished with a very prominent lobe at its infero-proximal angle; carpus usually a little longer than broad, a little longer than merus, considerably longer than palm, outer surface evenly convex, margins subparallel, acute and ciliate, upper margin produced into a thin expansion overhanging the smooth inner surface, lower margin similar but not nearly so strongly produced, posterior margin below the articulation of merus produced backwards into a prominent, broadly and evenly rounded lobe; hand narrower than and about the same length as carpus (usually a little longer), convex above; palm broader than long, broadest at base, with the ciliate margins more or less incurved toward the proximal end, upper margin serrulate only at distal end; fingers with a prominent hiatus between them; a prominent upturned tooth with a serrulate margin between bases of fingers; fingers a little longer than palm and furnished with tufts of hair; pollex evenly curved upward, denticulate on upper margin; dactyl slightly longer than pollex, bent abruptly near the tip, forming a sharp hook, lower margin minutely denticulate, upper margin more or less denticulate. In the small cheliped (adult male) the margins are almost entirely smooth; the ischium resembles that of the larger one but is scarcely if at all denticulate below; merus widest near middle, shorter than ischium, without basal lobe but having an obsolescent tooth near middle of lower margin; carpus very long and narrow, with both surfaces convex, margins parallel; hand of same width as carpus and of about same length; palm longer than wide, margins parallel; fingers ciliate but not gaping, longer than pollex and not hooked at tip. Small cheliped in female is like that of male but larger cheliped is relatively smaller and of a different form; the ischium is like that of the male and the merus quite similar but furnished with a somewhat less prominent inferior lobe; carpus is similar in shape to that of male but both surfaces are convex, margins not produced as in the male; hand as wide as carpus, palm about as broad as long with margins subparallel; fingers similar to male but a little shorter than palm. In both male and female the lobe at infero-proximal angle of merus of the large cheliped is almost completely covered when the carpus is bent at right angles to the merus. Ambulatory legs stout and more or less ciliate, particularly on hands; first, second and third pairs of ambulatory legs decidedly compressed, fourth but little compressed; first, second and fourth subequal in length, the third somewhat longer; first pair considerably longer than the carapace, with short broad hand, inner and outer surfaces with tufts of hair, margins

ciliate, fingers longer than palm, pollex and dactyl subequal at base or pollex slightly broader; lower margin of merus and upper and distal portions of lower margins of carpus ciliate; second pair with hand developed into a broad blade with a small dactyl; fourth and fifth with hand longer than broad. Telson slightly shorter than uropods and furnished with a rounded emargination at tip. Uropods distally truncate and slightly exceeding the telson.

Dimensions. Length of male specimen 61 mm, length of larger cheliped 50 mm, of smaller cheliped 32 mm; length of larger cheliped of female 31 mm, of smaller cheliped 28 mm (Holmes).

Color. In younger specimens the body is usually a delicate orange to deep rose-pink, the chelipeds and ambulatory legs are rose-pink, but sometimes the whole is quite a bright orange. In adult specimens the abdomen and ambulatory legs are lighter and the chelipeds are white.

Type Locality. "California."

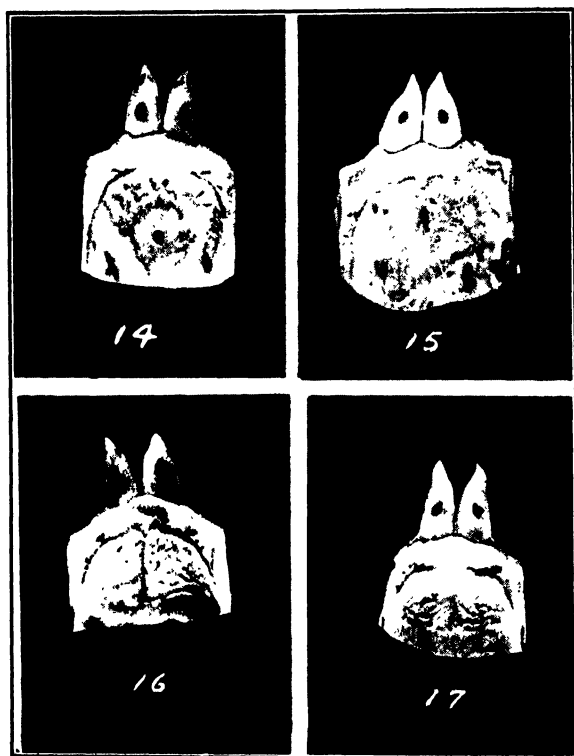
Distribution. From Mutiny Bay, Alaska (Lockington), to mouth of Tia Juana River, San Diego County, California (Rathbun).

Specimens have been examined by the author from the following locations: *British Columbia*: Locke Bay; Robert's Bay near Sidney, Tofino Inlet, Vancouver Island (in the collection at the University of British Columbia); *Washington*: beach at Jensen's shipyard southeast of Friday Harbor; Fox Cove, Sucia Island; Mabano and beach directly across on Camano Island; Sandy Point and Langley on Whidby Island; Allyn (about $\frac{3}{4}$ mile north of wharf); Seabeck and Union City on Hood Canal; Copalis; North Cove; *Oregon*: Coos Bay; *California*: Elk Horn Slough, Monterey Bay.

Remarks. The divergence of the eye-stalks has previously been indicated as a diagnostic characteristic in differentiating *californiensis* from *gigas* but in *californiensis* it is too variable to be considered as such. This is particularly true of specimens from Allyn, Seabeck and Camano Island, Washington. In these specimens the chelipeds are slightly more slender than is usual but otherwise they possess very decided *californiensis* characteristics. The degree of convexity of the median tooth of the front has also been used in separating these two species but the difference as shown in figs. 14-17 is too nearly imperceptible to be of any use in distinguishing them.

The large cheliped of *californiensis* in the male, up to about three-fourths grown, is very similar in form to that of the female, scarcely exhibiting the thin expansions of the margins of the carpus so very characteristic in the adult male.

In San Juan Islands the only locations where *californiensis* was taken are across from Fossil Bay, Sucia Island, where they are very numerous, and at Newhall's Beach where only one specimen, a male, was taken. Many *gigas* were collected at various times at Newhall's



Rostrum and eye-stalks of *Callianassa*.

Fig. 14. *C. gigas*, male. $\times 3$.

Fig. 15. *C. gigas*, female. $\times 3$.

Fig. 16. *C. californiensis*, male. $\times 3$.

Fig. 17. *C. californiensis*, female. $\times 3$.

Beach but this particular individual is unquestionably *californiensis*. By no means were all the beaches of the region visited but considerable territory is represented in the collection.

Only one case of obvious regeneration has been found in all the specimens of *Upogebia* and *Callianassa* examined. This is in a small male of *californiensis* in which the small cheliped is smaller than the ambulatory legs, very feeble and malformed.

Callianassa affinis Holmes. Fig. 18.

Callianassa affinis Holmes, Occas. Papers Calif. Acad. Sci. 7:162, pl. 2, figs. 29-30, 1900; Rathbun, H. A. E. 10:154, 1904; Schmitt, Univ. of Calif. Publ. in Zool. 23:119, fig. 81, 1921.

Characters. Front obscurely tridentate. Eye-stalks oblong, subacute, with inner extremities tuberculiform and not diverging toward the tip; cornea in front of the middle of the stalk. Antennule a little less than half as long as the antenna, flagella subequal. Antennae about half the length of the body, the peduncle nearly equal in length to that of the antennules. Eye-stalks reaching nearly to the end of the first antennular segment, little longer than wide, sides subparallel, inner extremities tuberculiform, not diverging towards the tip, pigmented cornea considerably in front of middle of stalk. Chelipeds in adult male very unequal. Large cheliped with ischium dentate below; merus stout, lower margin denticulate and furnished with a prominent lobe on the under side near the base; carpus very little longer than broad, and very little longer, sometimes even shorter,



Fig. 18 *Callianassa affinis* Holmes, male; left, small cheliped; right, large cheliped. (After Holmes).

than palm, postero-inferior angle broadly rounded and the margin not produced as it is in *californiensis*; hand fully twice the length of the carpus; palm oblong, both inner and outer surfaces convex; dactyl longer than pollex, the extremity hooked and the prehensile margin furnished with a few stout teeth. Small cheliped slender; merus widest at the middle; carpus narrow, as long as the hand; fingers pubescent. First pair of ambulatory legs ciliate below. Telson broadly rounded and shorter than uropods.

Dimensions. Of a male specimen from Point Loma, in the collection of the National Museum: length from tip of rostrum to end of telson 61 mm, of carapace 17 mm, of large cheliped 50 mm, of hand and fingers 16 mm, of carpus 8.5 mm, greatest width of hand 8 mm, and of carpus 9.5 mm (Schmitt).

Color. The author finds no record of color and has not examined live specimens.

Type locality. Point Loma, California.

Distribution. From Santa Monica Bay to San Diego, California (Rathbun).

Remarks. The above description is almost entirely adapted from preceding writers since the author has examined but six specimens, loaned by the Smithsonian Institution. Of these one male and one female were collected at Isthmus Harbor, Santa Catalina Island, California; three males and one female were collected between Government Breakwater and Point Fermin, San Pedro, California.

Callianassa goniophthalma Rathbun. Fig. 19.

Callianassa goniophthalma Rathbun, Proc. U.S. Nat. Mus. 24:886, 1902; H. A. E. 10:154, pl. 8, 1904; Schmitt, Univ. of Calif. Pub. in Zool. 23:121, fig. 82, 1921.

Characters. Median tooth of front sharp and prominent, reaches barely one-third the length of the eye-stalks, lateral teeth shallow and blunt. No median carina, but a slight blunt elevation near posterior margin corresponding to the strong tooth of *C. coecigena*. Eye-stalks reaching nearly to the end of the first antennular segment, more than twice as long as wide, sides subparallel, antero-external angle rounded, antero-internal angle produced in a tuberculiform tooth, these teeth being slightly divergent, eyes without pigment. Antennule with flagella subequal. Antennae with flagella nearly as long as the body, peduncle overreaching the antennular peduncle by the length of the last and one-third of the preceding segment. Chelipeds very unequal. Large cheliped equal in length to the carpus and the first four abdominal somites combined; ischium with a few minute spinules at proximal end of lower edge; merus may have a small spine at the proximal end of its lower margin, or it may (as in the largest specimen) be devoid of armature; carpus shorter than wide, nearly twice as deep as it is long and half as long as the palm, lower angle rounded; palm a little longer than high, subequal in length to dactyl, distal lower quarter with a few tubercles irregularly disposed from which proceed bunches of hair; fingers gape widely in male, not at all in female, in both beset with bunches of long hair; pollex with a stout tooth on upper edge; dactyl longer than pollex, upper surface very broad and with a rounded carina on inside and outside, outer surface tuberculate near base of finger, outer margin of cutting surface has a broad tuberculate tooth near palm and a lobe near tip, inner margin of cutting surface is tuberculate along its distal half; lower margin of ischium, merus and carpus and both upper and lower margins of hand are carinate. Small cheliped one-third as wide as the larger, reaches only to distal third of palm of larger; ischium

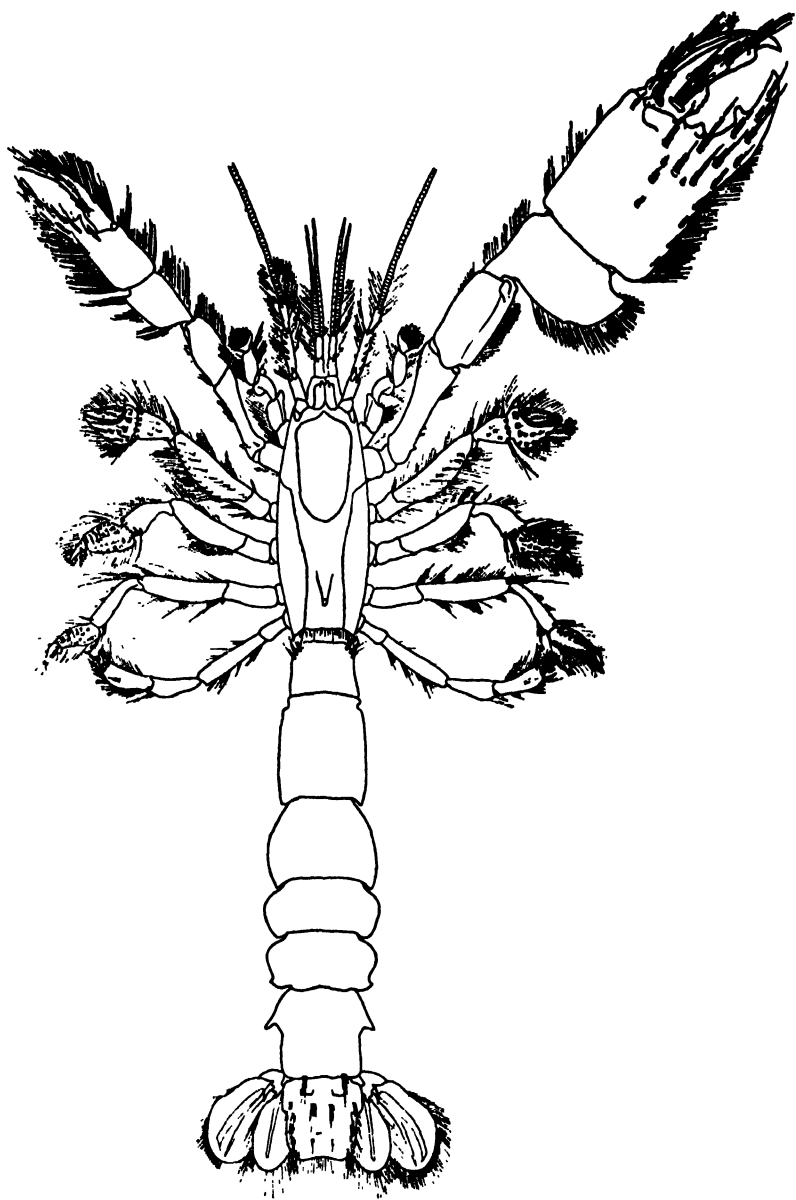


Fig. 19. *Callianassa goniophthalma* Rathbun, male, about natural size (After Rathbun).

and merus similar to those of the large cheliped; carpus longer than high, low angle subacute; palm a little shorter than carpus, longer than wide; fingers do not gape as they overlap far from the extremities; dactyl slender, nearly twice as long as palm and longer than pollex which is armed with a single sharp tooth at its proximal third. First, second and third pairs of ambulatory legs stout, compressed and increasing slightly in length in the order named; fourth pair as long as the second; first pair a little longer than carpus and ending in a short, broad, compressed hand, the edges and outer surface of which are setose, as are also the lower border of the merus and the upper and distal borders of carpus; dactyli of remaining pairs almost hidden in setae. Telson nearly as long as sixth abdominal somite; sides subparallel, notched at anterior third; posterior angles rounded. Uropods broad and rounded, the outer much the larger.

Dimensions. Type, male: length of carpus 30.5 mm, of abdomen 67.5 mm; female: length of carapace 22.2 mm, of abdomen 52 mm.

Color. The author finds no record.

Type locality. Off Point Conception, California, 513 meters ("Albatross" Station 3198).

Distribution. Also taken by the "Albatross" in Clarence Strait, Alaska, 595 meters, and off Harris Point, San Miguel Island, California, 487-500 meters (Schmitt).

Remarks. Closely allied to *C. coccigena* Alcock and Anderson, but differs in the shorter rostrum, in the absence of spines on the second to fifth somites of the abdomen, in the squarer telson. The shape of the first pair of chelipeds is the same as in *C. coccigena*, but the carpus of the larger one is without a spine, the palm is not serrate on its lower margin; its outer surface is furnished with tubercles on the distal lower quarter, to which also the hairs are restricted; pollex is shorter in our species and its tooth is nearer the middle (Rathbun).

The above description is adapted from preceding writers since the author has examined but three specimens of this species, loaned by the Smithsonian Institution. Of these two males and one female were collected in the vicinity of Funder Bay, Lynn Canal, Alaska, 549-573 meters "Albatross" Station 4258.

ÉCOLOGICAL OBSERVATIONS

Upogebia pugettensis is commonly found at about mean low tide on muddy beaches free from *Zostera* where there is more or less gravel. They have, however, been brought up in the dredge from several meters; they have been found ranging upward almost to high water and they have been taken in very compact clay and gravel. Occasionally they have been observed crawling over the surface but ordinarily one might walk over an area thickly inhabited by them without suspecting their presence, except for the openings to the burrows and the mounds thrown up in the process of excavation. The openings may be confused easily with those of some of the larger clams, and the mounds with those of some of the worms, but a clam opening usually has little if any mound about it, and a worm mound has no large burrow beneath it. As the burrows of *Upogebia pugettensis* are found when the tide is out, there is usually a plug of loose gravel at the opening. This plug extends down from the top to the base of the mound, a distance of about 5 cm. Probably the finer material is washed away by the action of the water.

Considerable observation of burrows was made in connection with digging out specimens but this, except for information concerning the general trend of the subterranean passage, was very unsatisfactory. There was a great tendency for the excavation to fill up with water, and the earth to cave in, thus obscuring the course of the particular burrow in question. Flexible branches of willow were run down the passageway and helped to identify the course near the surface, but deeper, the difficulties above mentioned were again encountered. Cement was poured into a few burrows in an attempt to mark their courses in that way but it also was unsatisfactory since it was practically the same color as the earth and in addition much of it oozed out thru the spaces between the gravel before hardening. Plaster of paris served the purpose very well since it hardened quickly and was easily seen, for even tho it mixed with the sand to a slight degree it remained nearly white. The only difficulty encountered in this method was in filling the burrow rapidly enough so that the plaster of paris did not harden before reaching the surface at the other opening or openings. A very thin paste was mixed in quantities of about one quart and poured immediately. One person mixed the paste while the other poured it. At the next sufficiently low tide, the cast was dug up and examined. To avoid breaking, it was necessary to remove it in sections and then rejoin these with a little freshly mixed plaster of paris. The largest burrow (fig. 20) explored

in this way by the writer extended to a depth of about 1 meter. Needless to say, the labor involved in excavating such a cast prohibited many repetitions of the experiment.

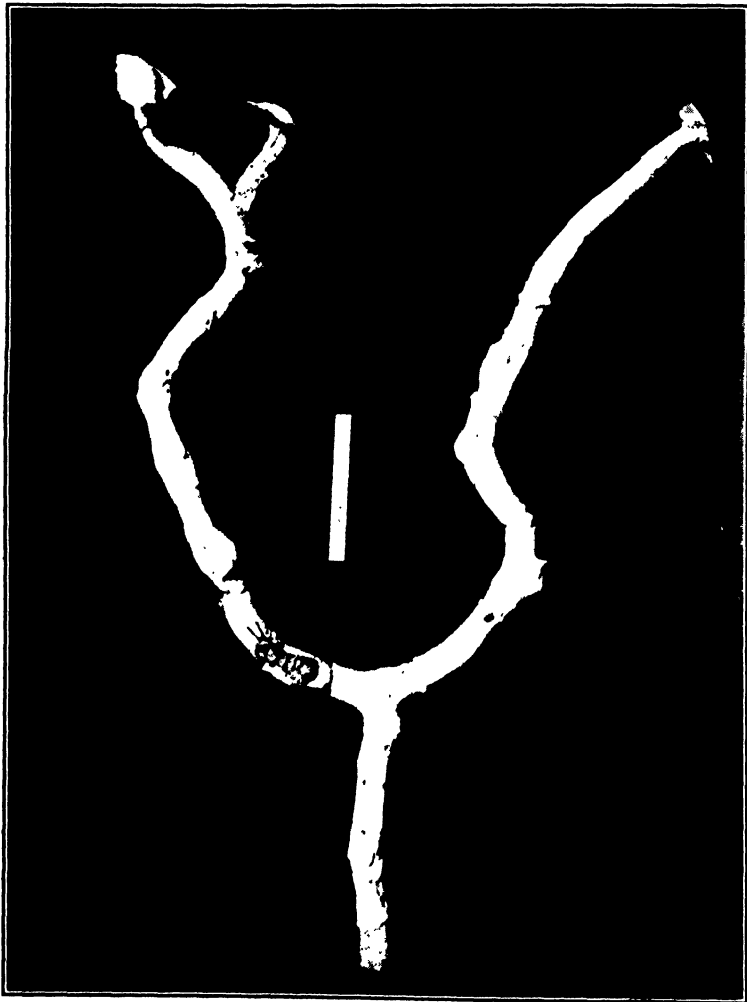


Fig. 20. Burrow of *Upogebia pugettensis* (plaster of paris cast), \times about .13.

The burrows are quite cylindrical and range in depth from several centimeters to about 1 meter. The diameter varies, of course, with the size of the animal but for the most part it is from 2 to 4 cm. The burrows are nearly vertical and are in a general way Y-shaped

or U-shaped with two or more branches opening at the surface and with one or sometimes more short, blind passages extending down or to the side. Some burrows, apparently in the initial stages of construction, consist of only one nearly straight channel. The longest of this sort examined extended, for the most part straight down, to a depth of .8 meter with but one very slight extension to the side.

At regular intervals of about 15 cm, or about the full length of the animal from the tip of the telson to the tip of the chelipeds, the burrow undergoes a slight curvature. This may be accounted for by the method of excavation employed which involves a queer sort of somersault in order to reverse the position after digging. A *Upogebia* was placed in a battery jar of gravel, sand and mud from the beach and its activities observed, as described below.

The load is scooped up by the third maxillipeds which are strong and pediform. A carrier is formed by the chelipeds and the first pair of walking legs. To form the sides the chelipeds are extended straight forward, about 1 cm apart with a large load. The first pair of walking legs, with their inner margins provided with rows of long interlaced hairs reenforced by shorter ones, are turned in to form a very efficient bottom. When the load is ready, the tail is well flexed and the animal turns over on its side, at the same time moving the chelipeds and the anterior end back toward the tail. As the tips of the chelae pass the tail it begins to extend in the opposite direction. When the chelae are a little beyond the tail, the animal continues its turning on the side, at the same time extending the tail in one direction and the chelae in the opposite until it lands in a normal position fully extended and headed toward the opening. In turning, the last three pairs of legs scrape the tail, thus aiding in the somersault. The whole performance takes about 10 seconds and is very gracefully done without losing the load of loose material to be transported to the surface. Then the animal moves forward with a fair degree of rapidity. In moving forward, the animal uses the chelipeds and walking legs, the tail dragging fully extended. Backward locomotion is accomplished by the additional use of the tail which is flexed and then partly extended. The turning may account in part at least for the cylindrical form of the burrow. As a result of the pressure of the animal's body in the great many trips back and forward, the walls are smooth as if plastered.

At the surface the load is shoved off by working the chelipeds and the first pair of ambulatory legs back and forth alternately. A big load amounts to about a teaspoonful.

The second walking leg, provided with a row of several long, sharp teeth curved forward, is used very effectively as a combination brush and comb for the fore part of the body. An occasional circulation of the water is produced by the rhythmical backward and forward motion of the four leaf-like pleopods. Both pairs diverge at the same time but the inner pair start back when the outer is about half way out, and vice versa, at the rate of about once a second. This creates a circulation in the water which is very apparent out to a distance of about 2.5 cm from the body of the animal.

The observations made of *Callianassa* are more casual than those of *Upogebia*. No casts were made of *Callianassa* but, judging from observations noted while collecting specimens, the burrows are very similar to those of *Upogebia*. They are, however, constructed in more finely divided material and the mound consequently lacks the plug of gravel usually present in the opening of that of the *Upogebia*. In locomotion *Callianassa* ordinarily carries the large cheliped flexed so that it is about equal in length with the smaller, which is extended straight forward. Sometimes, however, the animal travels with this seemingly cumbersome appendage extended to full length. The pads of hair on the hands of the last two walking legs serve as brushes in cleaning the body. The animal is very agile in wielding them and can even scrub the basal joints of the same appendage. They may be used singly or together in thoroughly brushing out the gills. They may also be operated on the same or on the opposite side of the body.

To ascertain what they eat, the writer examined several *Upogebia* and *Callianassa*. Their food, so far as could be determined, consists of plant debris and a very few diatoms. The great mass of material in the digestive tract consists of fine grains of sand.

ECONOMIC RELATIONS

The *Callianassidae*, popularly known as "crawfish," "mud prawns," "ghost shrimps," or "burrowing shrimps," are reported to be a great menace to the oyster industry of the Pacific Coast. In fact, Professor Kincaid has said to the writer that, in connection with his investigation of various oyster beds, he has come to consider them the worst enemy of the native oyster, *Ostrea lurida* Carpenter. The starfish, *Pisaster ochraceus* (Brandt) and *Evasterias troschelli* (Stimpson) are well known to be very destructive to oysters. It is, however, comparatively simple to combat these since they live above ground and may easily be seen and removed. The moon snail, *Polinices lewisii* (Gould), another enemy of the oyster, living above

ground, is easily killed by crushing. But owing to the subterranean habits of the *Callianassidae* and to the methods of culture necessary for growing *O. lurida*, these "crawfish" are far more difficult to cope with than the other enemies mentioned. There is a considerable area at Oyster Bay, Rocky Bay and at Little Skookum where they do a great deal of damage. Some regions like Nahcotta on the west side of Willapa Harbor where oysters were formerly abundant are now not worth working on account of the depredations of this pest; others very suitable for oyster culture have not been developed, largely because the *Callianassidae* are present.

The destruction is really two fold: (1) the smothering of the young oysters with material thrown up in the process of excavation of the burrows, and (2) the draining of the dikes which exposes the beds to drying and is consequently fatal to both young and adults.

In the excavation of their burrows both *Callianassa* and *Upogebia* throw up small mounds of sand and debris. These mounds are about 10 to 20 cm in diameter and about 3 to 8 cm high. The size of the mound varies, of course, with the kind of material. *Callianassa* is usually found in mud and sand but can work its way thru the spaces between gravel and boulders. *Upogebia* inhabits areas made up of coarser and often more compact material. On the west side of Brown Island, *Upogebia* has been observed to be quite numerous in a bed of clay so hard that it is very difficult to penetrate it even with an ordinary shovel. However, the greatest activity is carried on in ground that is quite sandy. In loose sand the young up to a length of about 4 cm are frequently found crawling about to a depth of several centimeters with no apparent burrows, but later very definite burrows are excavated. The mounds, thrown up at the openings of the burrows, by the nature of their construction are not compact, and consequently their material is easily scattered by the action of the tides.

A natural oyster bed is fairly well protected against the *Callianassidae*. It is a matting of oyster shells, mussels, fine shells and various debris. This mat is called the cultch and may be 15 to 20 cm thick. As oysters die their shells are added to this. In the natural bed the live oysters were in the upper strata and not easily harmed. But in oystering, the cultch was in earlier times taken up and carried to the shore where the oysters were sorted out. Nothing was put back. After the removal of the cultch the "crawfish" came in and mined all thru the area. In this way they have taken practically complete possession of many acres. This condition exists in Willapa

Harbor where in some cases the mounds are so numerous that their bases overlap. The oyster spat attach to the shells of the bottom and thereby fall easy victims to the operations of this pest. They are soon buried to the depth of several centimeters and die as a result of suffocation. The adult oysters may blow the stuff out for a time, but even a thin layer creates an anaerobic condition too difficult for the spat to overcome.

The second method of destruction for which the "crawfish" are responsible is more indirect than the first but just as certain. Naturally oysters grow at about mean low tide. For convenience in culture, oystering along the Pacific Coast is done from medium down to mean low tide. Thus in order to keep the beds from being exposed during very low tides it is necessary to construct dikes. These consist of low cement or wooden walls around the beds to hold a thin layer of water over the oysters. The burrows of the Callianassidae sometimes descend to a depth of 1 meter and are Y-shaped, one channel coming to the surface inside of the dike and the other on the outside. When the tide goes out this combination acts as a very effective system of drain pipes and the oysters are exposed.

Some oyster growers have made futile efforts to protect their beds by covering them with a layer of gravel or shell before planting the oysters. This is obviously a very unsubstantial barricade against such persistent burrowers. Various oyster men have reported that it takes the "crawfish" only about 1 year to bury quite completely the gravel, shell and oysters of a newly planted area.

Basalt and broken rock would form an impassable barrier but the expense involved is prohibitive. The same is true of cement.

The native oyster, *O. lurida*, will not attach to brush as will the Japanese oyster, *O. gigas* Thunberg, and the eastern oyster, *O. virginica* Gmelin. Consequently this device, which might be used to raise the spat above the invested areas, is useless as a means of relieving the situation here.

Up to the present time, according to Professor Kincaid, the most effective defense which has been developed is a double board floor such as is used over a small area at Little Skookum on Willapa Harbor. The material of the beach is shoveled off to a depth of 10 to 12 centimeters. Over this area a board floor of rough lumber is laid, which in turn is covered by another similar floor laid at right angles to the first. Then the previously removed surface material is spread out over this. No cracks are left and the Callianassidae cannot burrow thru the boards. Boarding may make possible the use of

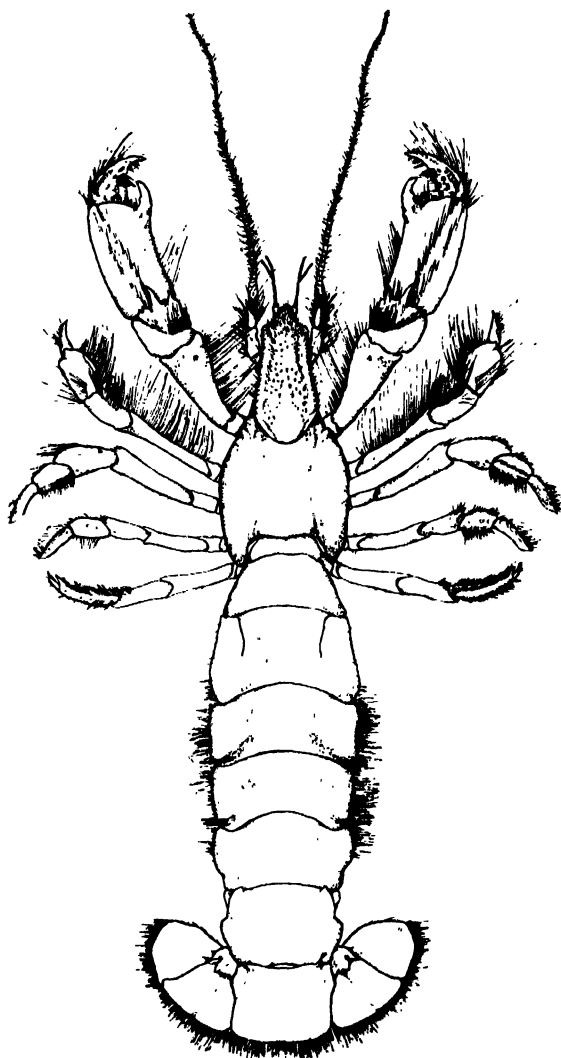


Fig. 21. *Upogebia pugettensis* (Dana), male, dorsal view. $\times 1$.

some areas not now under cultivation, but the initial expense is large and renders this plan not very practical. However, the boards are fairly permanent, since they are buried beneath several centimeters of sand and gravel and thus suffer little depreciation thru attack of wood borers.

Owing to their subterranean habits, there seems to be as yet no really adequate and at the same time economical method of coping with the Callianassidae.

Upogebia pugettensis (Dana); drawings $\times 3$.

bp - basipodite	en - endopodite	mp - meropodite
cp - carpopodite	ex - exopodite	pp - propodite
cx - coxopodite	fl - flagellum	sc - scaphognathite
dp - dactylopodite	ip - ischiopodite	

Fig. 22. Left first antenna (antennule), outer side.

Fig. 23. Left second antenna, outer side.

Fig. 24. Left mandible, ventral.

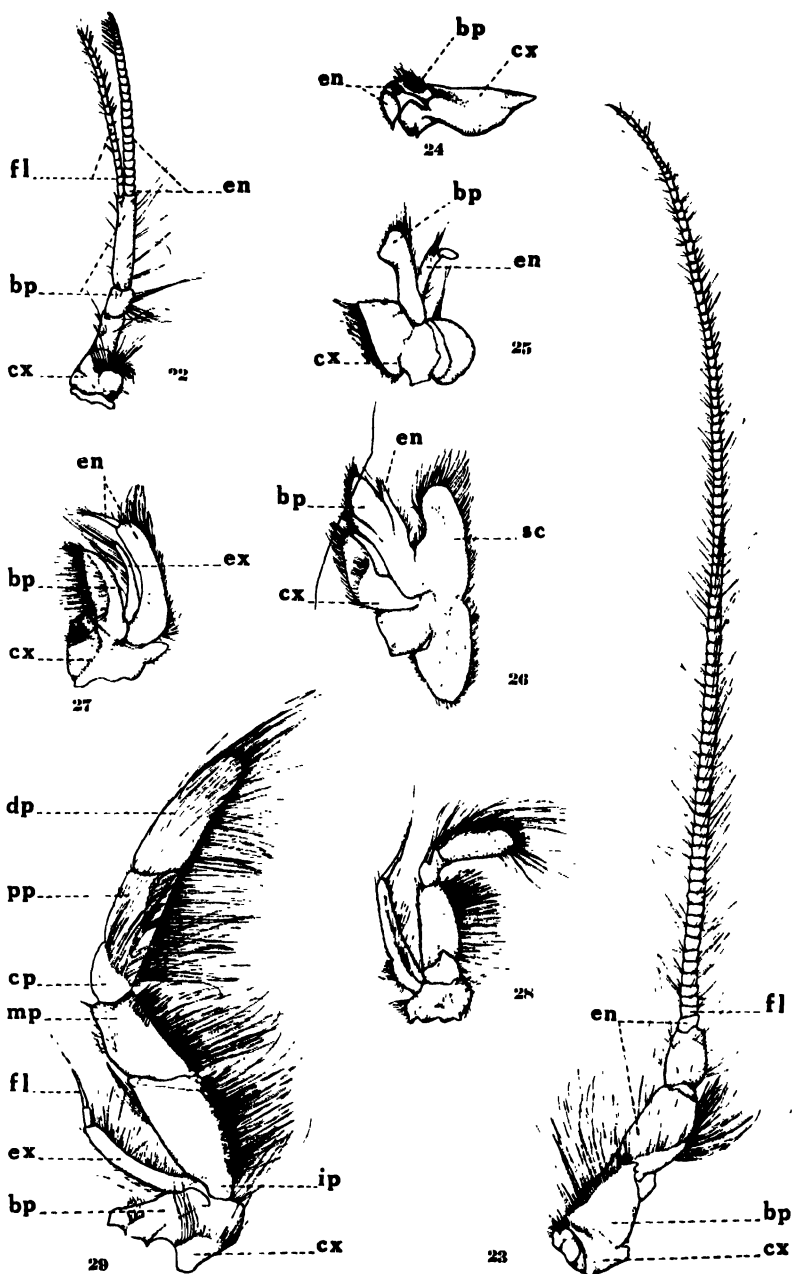
Fig. 25. Left first maxilla, ventral.

Fig. 26. Left second maxilla and scaphognathite, ventral.

Fig. 27. Left first maxilliped, ventral.

Fig. 28. Left second maxilliped, inner side.

Fig. 29. Left third maxilliped, inner side.



UROGEBIA PUGETTENSIS

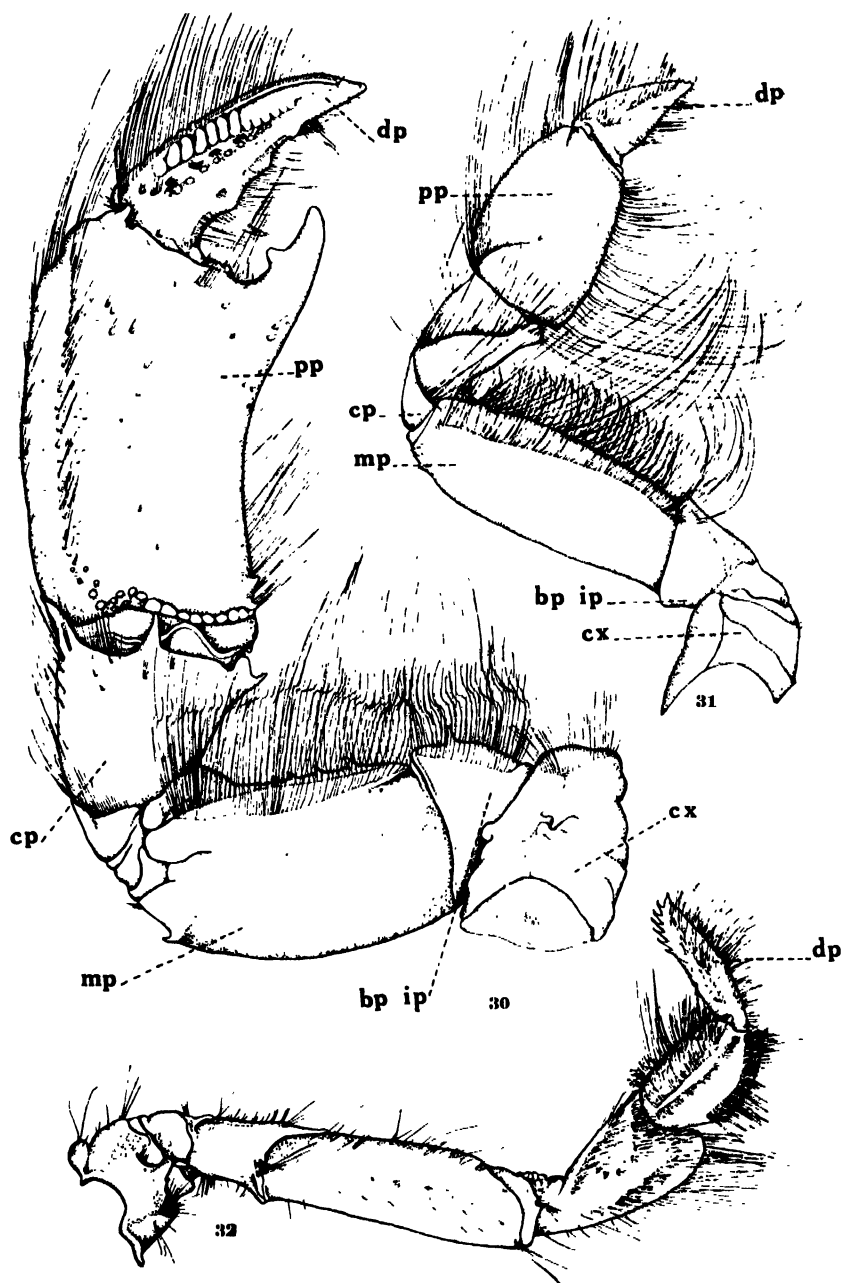
Upogebia pugettensis (Dana) ; drawings $\times 3$.

lp - basipodite	dp - dactylopodite	mp - meropodite
cp - carpopodite	ip - ischiopodite	pp - propodite
cx - coxopodite		

Fig. 30. Left cheliped, inner side.

Fig. 31. Left second pereopod (ambulatory leg), inner side.

Fig. 32. Left third pereopod, outer side.



UROGEBIA PUGETTENSIS

Upogebia pugettensis (Dana); drawings $\times 3$.

bp - basipodite	en - endopodite	mp - meropodite
cp - carpopodite	ex - exopodite	pp - propodite
cx - coxopodite	ip - ischiopodite	pt - protopodite
dp - dactylopodite		

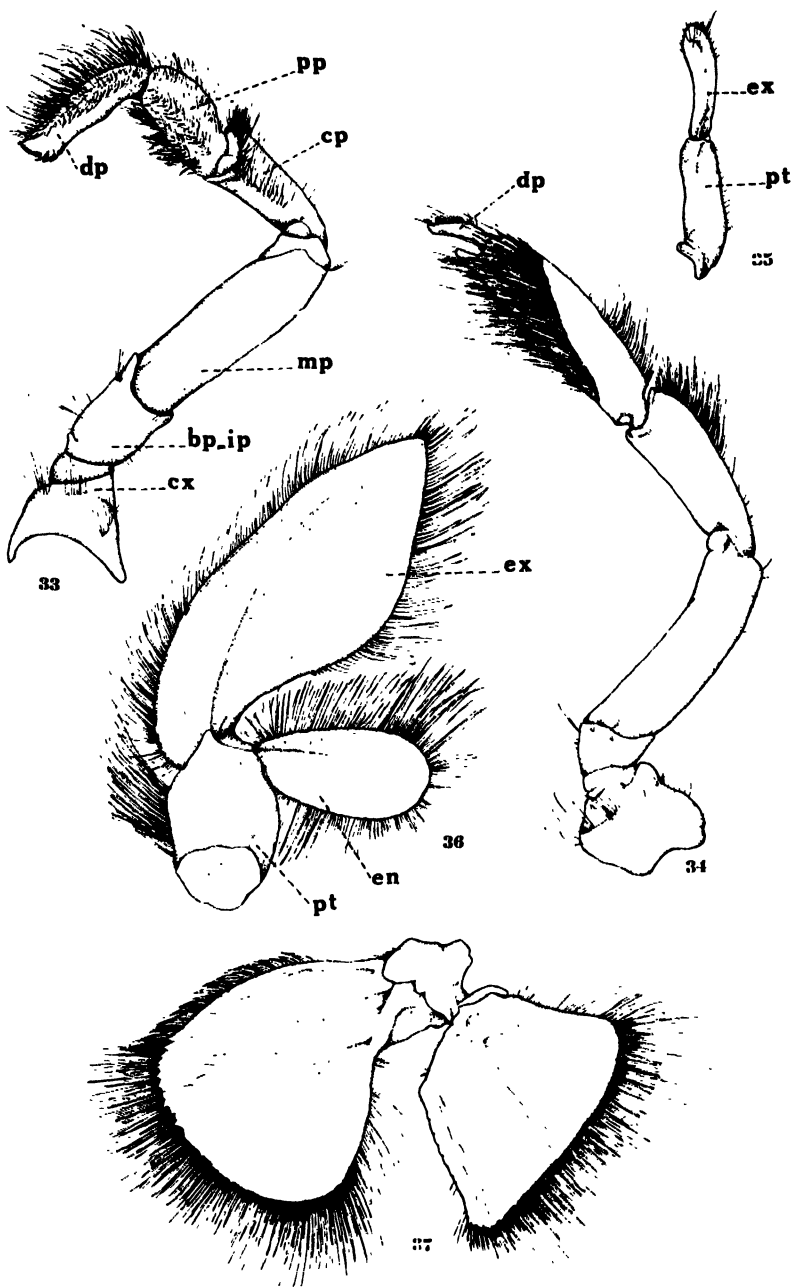
Fig. 33. Left fourth pereopod, outer side.

Fig. 34. Left fifth pereopod, outer side.

Fig. 35. Left first pleopod, female, ventral.

Fig. 36. Left first pleopod, male, (female similar), dorsal.

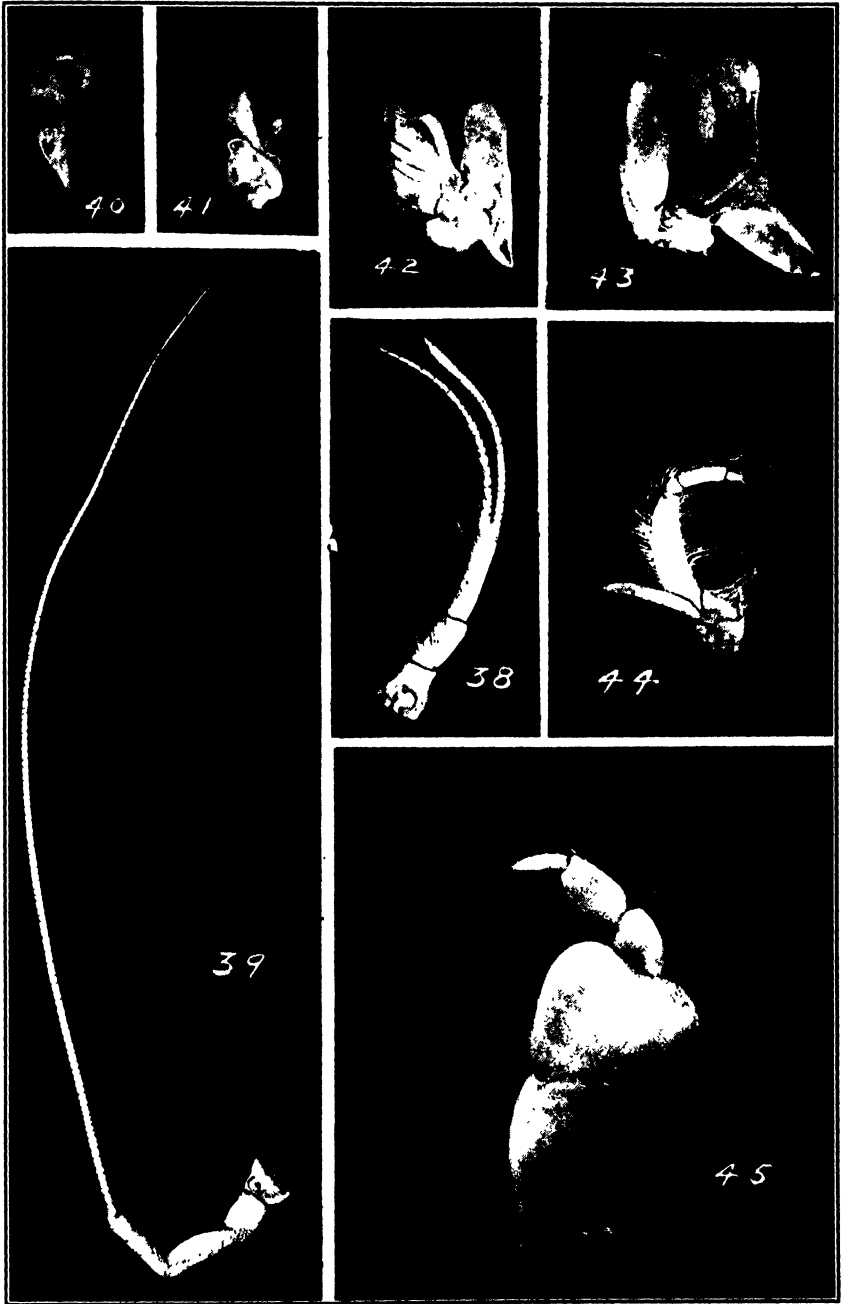
Fig. 37. Left uropod, dorsal.



UROGEBIA PUGETTENSIS

Callinassa gigas Dana; photographs $\times 3$.

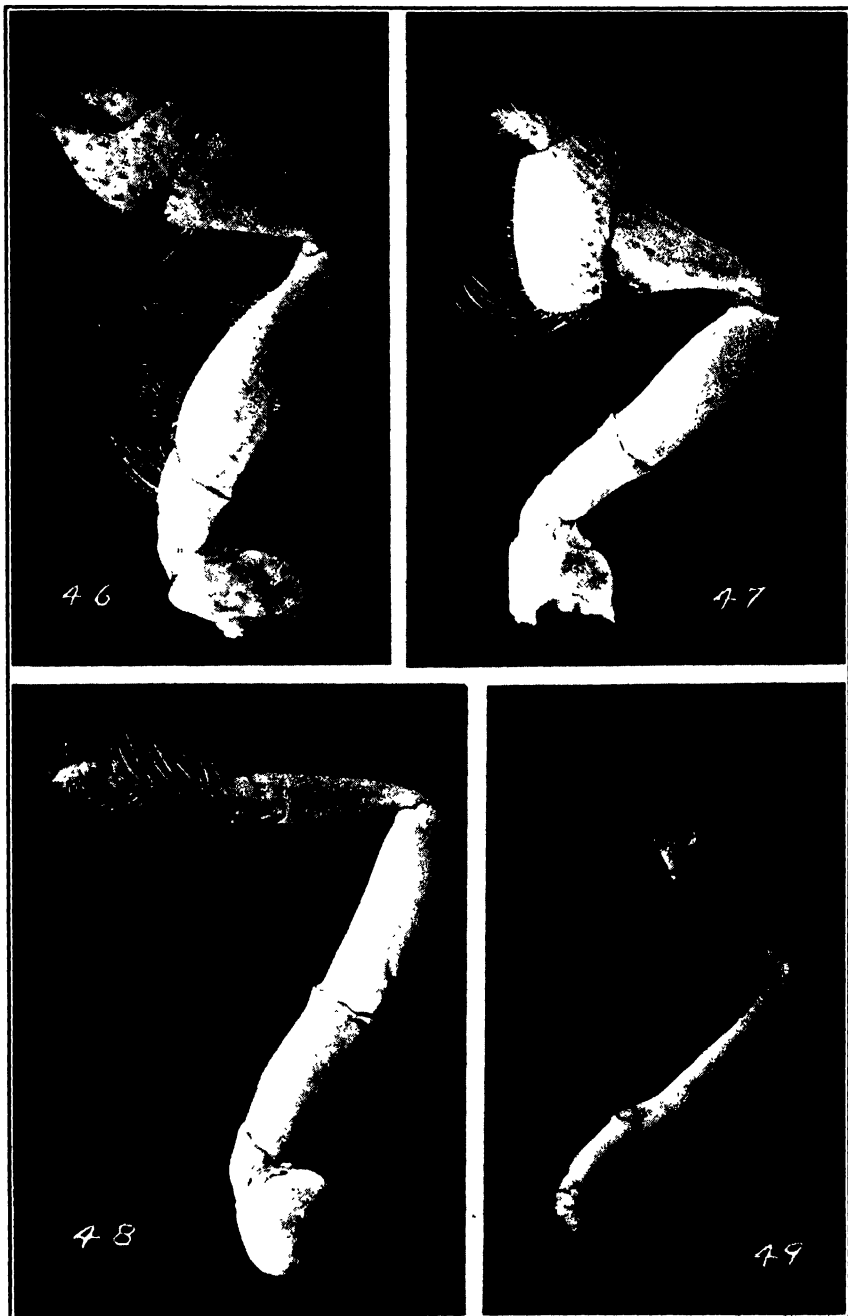
- Fig. 38. Left first antenna (antennule), outer side.
- Fig. 39. Left second antenna, lateral, outer side.
- Fig. 40. Left mandible, ventral.
- Fig. 41. Left first maxilla, ventral.
- Fig. 42. Left second maxilla and scaphognathite, ventral.
- Fig. 43. Left first maxilliped, ventral.
- Fig. 44. Left second maxilliped, inner side.
- Fig. 45. Left third maxilliped, outer side.



CALLIANASSA GIGAS

Callianassa gigas Dana; photographs $\times 3$.

- Fig. 46. Left second pereiopod (ambulatory leg), outer side.
- Fig. 47. Left third pereiopod, outer side.
- Fig. 48. Left fourth pereiopod, outer side.
- Fig. 49. Left fifth pereiopod, outer side.



CALLIANASSA GIGAS

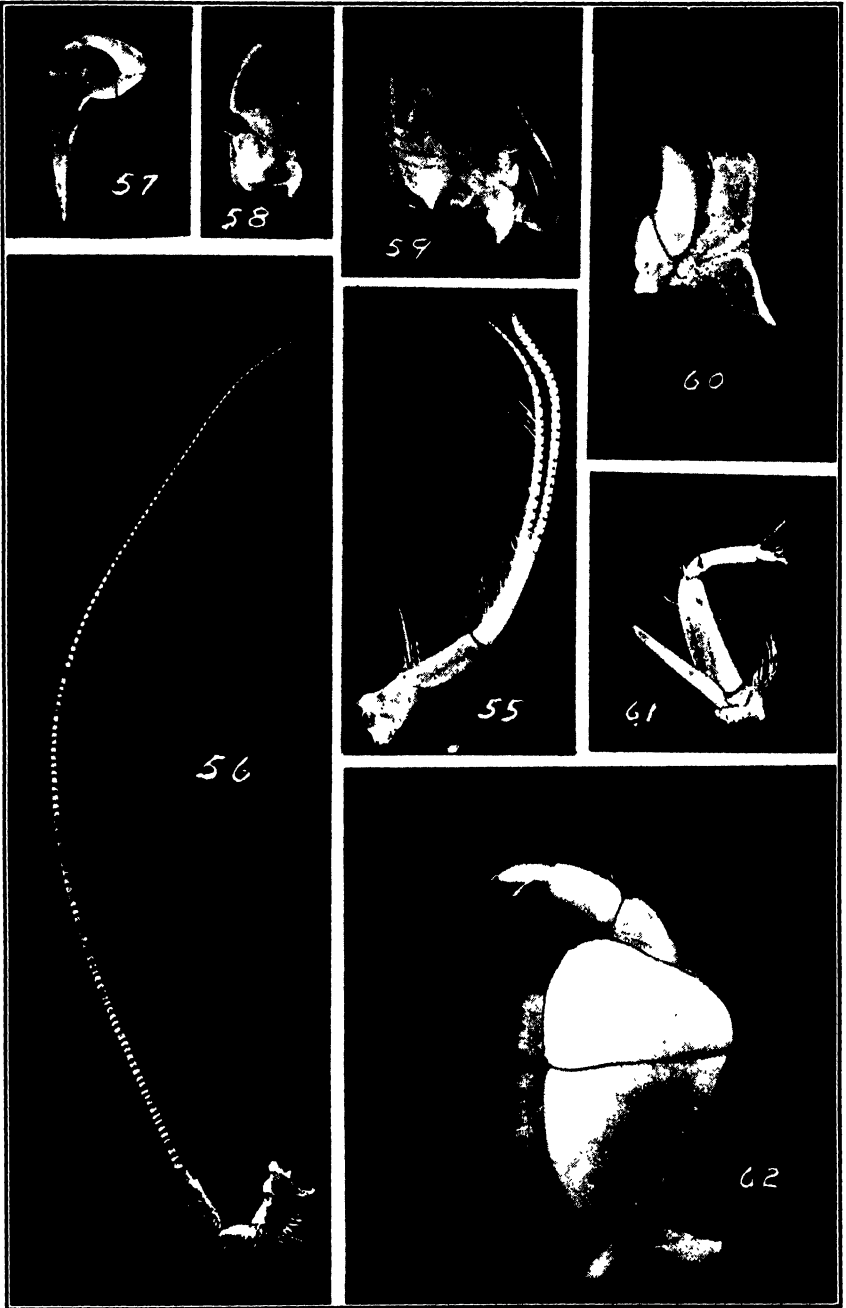
Callianassa gigas Dana; photographs $\times 3$.

- Fig. 50. Left first pleopod, female, ventral.
- Fig. 51. Left first pleopod, male, ventral.
- Fig. 52. Left second pleopod, female, ventral.
- Fig. 53. Left third pleopod, male (female similar), ventral.
- Fig. 54. Telson and uropods, dorsal.

*CALLIANASSA GIGAS*

Callianassa californiensis Dana; photographs $\times 3$.

- Fig. 55. Left first antenna (antennule), outer side.
- Fig. 56. Left second antenna, outer side.
- Fig. 57. Left mandible, ventral.
- Fig. 58. Left first maxilla, ventral.
- Fig. 59. Left second maxilla and scaphognathite, ventral.
- Fig. 60. Left first maxilliped, ventral.
- Fig. 61. Left second maxilliped, inner side.
- Fig. 62. Left third maxilliped, outer side.



CALLIANASSA CALIFORNIENSIS

Callianassa californiensis Dana; photographs $\times 3$.

Fig. 63. Left second pereiopod (ambulatory leg), outer side.

Fig. 64. Left third pereiopod, outer side.

Fig. 65. Left fourth pereiopod, outer side.

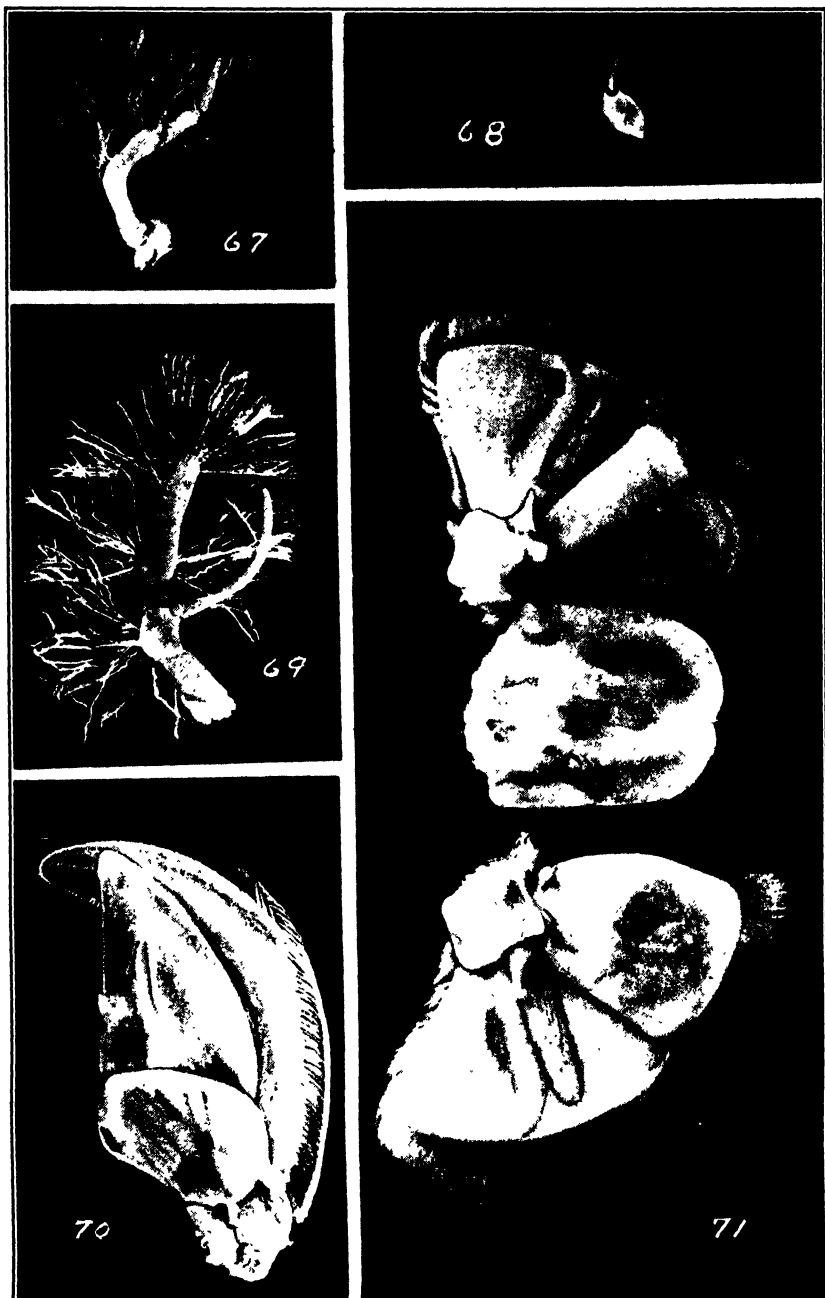
Fig. 66. Left fifth pereiopod, outer side.



CALLIANASSA CALIFORNIENSIS

Callianassa californiensis Dana; photographs $\times 3$.

- Fig. 67. Left first pleopod, female, ventral.
- Fig. 68. Left first pleopod, male, ventral.
- Fig. 69. Left second pleopod, female, ventral.
- Fig. 70. Left third pleopod, male (female similar), ventral.
- Fig. 71. Telson and uropods, dorsal.

*CALLIANASSA CALIFORNIENSIS*

The Sea Water at the Puget Sound Biological Station from September, 1926 to September, 1927

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INTRODUCTION

The purpose of this paper is to supply data concerning the seasonal variations in temperature, in chlorinity, and in the density of the sea water at the Puget Sound Biological Station, likewise in the quantity of plankton in this water. The original plan of this investigation covered a period of several years and publication was not anticipated until the end of that time; however there has been a demand for many of the data collected thus far, so it was deemed advisable to present them in a form readily available as the work for each successive year is completed.¹

COLLECTION OF THE SAMPLES

The samples showing the hourly variations at the surface were collected at the Station thru a complete tidal cycle in 1926 (Blacklock and Thompson, 1928) and again in 1927 (Thompson, Miller, Hitchings and Todd, 1929), while those for the study of the daily and weekly variations were secured in the channel at a point midway between the Station float and Brown Island. Both surface and depth samples were taken in the channel. The depth samples were collected with the Ekman reversing water bottle.

The chlorinity per liter at 20° was determined by Mohr's method and then converted by means of tables to grams per kilo, using the method outlined by one of us (Thompson, 1928). From the chlorinity per mille and the temperature, the actual specific gravity, σ_t , was calculated from the Hydrographical Tables.

The thermometers used in the depth measurements were of the reversing type and were attached to the water bottle. Surface tem-

¹ For the year 1927-28 data are being collected to show the variation in the dissolved oxygen and the pH.

TABLE 1. Hourly variations in temperature, chlorinity and specific gravity over two complete tidal cycles.

Time	August 12 and 13, 1926				August 20 and 21, 1927			
	Temperature °C	Chlorinity		Specific gravity σ_t	Temperature °C	Chlorinity		Specific gravity σ_t
		Per liter 20°C	Per kilo			Per liter 20°C	Per kilo	
8:00 P.M.	12.3	17.25	16.89	23.08	10.9	17.00	16.65	22.99
9:00	11.9	17.25	16.89	23.16	10.9	17.03	16.68	23.05
10:00	11.4	17.33	16.96	23.35	10.8	17.04	16.69	23.08
11:00	11.5	17.29	16.93	23.28	10.8	16.97	16.62	22.98
12:00	11.5	17.25	16.89	23.23	10.7	16.99	16.64	23.00
1:00 A.M.	11.5	17.25	16.89	23.23	10.7	16.97	16.62	23.00
2:00	11.5	17.25	16.89	23.23	10.7	16.97	16.62	23.00
3:00	11.5	17.21	16.85	23.17	10.8	16.92	16.57	22.90
4:00	11.5	17.21	16.85	23.17	10.9	17.01	16.66	23.00
5:00	11.6	16.99	16.64	22.86	10.9	17.04	16.69	23.07
6:00	11.6	17.17	16.81	23.11	10.8	17.04	16.69	23.09
7:00	11.7	17.17	16.81	23.13	11.0	16.96	16.61	22.93
8:00	11.8	17.15	16.79	23.04	10.9	16.91	16.56	22.88
9:00	12.2	17.21	16.85	23.05	11.0	17.02	16.67	23.02
10:00	12.5	17.15	16.79	22.90	11.2	17.01	16.66	22.96
11:00	12.6	17.19	16.83	22.94	11.3	17.04	16.69	23.00
12:00	12.6	17.25	16.89	23.03	11.3	17.18	16.82	23.18
1:00 P.M.	12.3	17.21	16.85	23.03	10.9	17.27	16.91	23.37
2:00	12.0	17.25	16.89	23.14	11.0	17.27	16.91	23.35
3:00	12.0	17.23	16.87	23.11	12.1	17.21	16.85	23.06
4:00	12.3	17.21	16.85	23.03	12.1	17.20	16.84	23.04
5:00	12.2	17.23	16.87	23.07	11.6	17.16	16.80	23.08
6:00	12.3	17.19	16.83	23.00	11.2	17.15	16.79	23.14
7:00	11.5	17.16	16.80	23.10	11.1	17.10	16.75	23.10
8:00	11.8	17.26	16.90	23.19	11.0	17.07	16.72	23.08

peratures were obtained with a thermometer graduated to 0.1° . The instruments were all calibrated before they were used.

EXPERIMENTAL PROCEDURE

Hourly Variations

A study of the surface water of two complete tidal cycles, in which samples were taken for a period of 25 hours, was made in

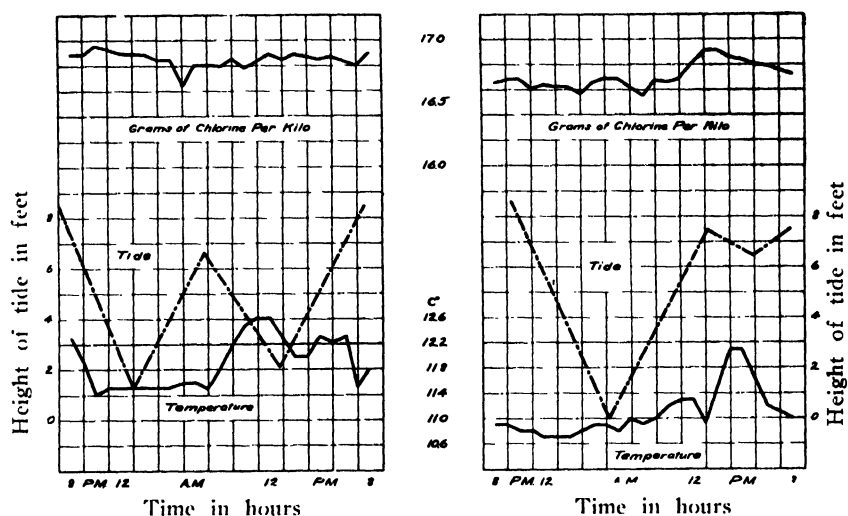


Fig. 1. Hourly variations of the surface sea water off the Puget Sound Biological Station for 1926 and 1927.

TABLE 2. Mean and maximum and minimum conditions of two complete tidal cycles.

	Tempera- ture °C	Chlorinity		Specific gravity σ_t
		Per liter 20°C	Per kilo	
August 12 and 13, 1926				
Maximum.....	12.6	17.33	16.96	23.35
Minimum.....	11.4	16.99	16.64	22.86
Difference.....	1.2	0.34	0.32	0.49
Mean.....	11.9	17.21	16.85	23.10
August 20 and 21, 1927				
Maximum.....	12.1	17.27	16.91	23.37
Minimum.....	10.7	16.91	16.56	22.88
Difference.....	1.4	0.36	0.35	0.49
Mean.....	11.1	17.06	16.71	23.06

August, 1926 and 1927. The data obtained are given in table 1 and graphically shown, together with the heights of the tides² corrected for Friday Harbor, in figure 1.

In table 2 are given the mean and the maximum and minimum conditions for the two tidal cycles. A study of the tables and graphs will show the following:

1. The temperature and the chlorinity of the waters were generally higher for the 1926 cycle than for the one studied in 1927. This was also true for mean conditions, excepting the means of the densities, which were practically identical.

2. The differences between extreme conditions for the two tidal cycles were much the same.

3. The greatest difference in the chlorinity was 0.35 ‰ or a maximum variation from the mean of 1.2%.

4. Maximum and minimum conditions for all three factors determined were either a function of the tide or the time of day. The higher temperatures were recorded within several hours of noon, in one case at the lower low water of late forenoon, and in the other at the lower high water of early afternoon.

Daily Variations

From June 19, 1927 to August 20, 1927 samples of water from the channel midway between Brown Island and the Puget Sound Biological Station were secured twice daily at the surface, and at the bottom in a depth of 12.8 meters. The data obtained are given in table 3 and graphically shown in figures 2 and 3. In table 4 are given the mean and the maximum and minimum conditions observed during this period of study. An examination of the tables and the graphs reveals the following:

1. In general the temperature is inversely proportional to the chlorinity.

2. There were two very marked variations in the condition of the sea water during the summer period. These occurred during the last week of July and again during the first weeks of August. The changes at the surface were very much greater than those en-

² There appears to be considerable doubt among the inhabitants of the San Juan Islands as to the correctness of tidal predictions for certain parts of the archipelago. The authors have made their calculations from the Tide Tables of the United States Coast and Geodetic Survey.

TABLE 3. *Daily variations of conditions of sea water over a two month period.*

Date 1927	Time	Tide	Surface				Depth of 12.8 meters				
			Temperature		Specific gravity σ_t	Chlorinity		Tempera- ture water	Chlorinity		Specific gravity σ_t
			Air	Water		Per liter 20°C	Per kilo		Per liter 20°C	Per kilo	
6-19	1:35 P.M.	Low	25.0	11.2	16.10	15.79	21.75	10.0	16.91	16.56	23.02
6-20	3:40	Flood	24.0	12.3	16.38	16.05	21.93	10.3	16.79	16.45	22.82
6-21	8:30 A.M.	Ebb	20.0	11.6	16.26	15.94	21.89	9.8	17.01	16.66	23.19
6-22	8:30	High	15.8	10.7	16.66	16.32	22.57	10.0	16.93	16.58	23.05
6-22	7:00 P.M.	Flood	13.5	10.8	16.75	16.41	22.68	10.1	16.85	16.50	22.92
6-23	8:15 A.M.	Flood	18.9	10.9	16.74	16.40	22.65	9.9	16.93	16.58	23.07
6-23	7:20 P.M.	Flood	13.8	10.6	17.01	16.66	23.06	10.0	17.01	16.66	23.17
6-24	7:45 P.M.	Flood	12.7	10.5	17.07	16.72	23.17	9.9	17.10	16.75	23.31
6-25	8:30	Flood	16.4	10.3	17.11	16.76	23.26	9.8	17.15	16.79	23.38
6-26	8:00 A.M.	Low	13.5	10.3	17.17	16.81	23.33	9.6	17.21	16.85	23.50
6-26	7:20 P.M.	*Low	12.7	10.3	17.25	16.89	23.42	9.7	17.33	16.96	23.65
6-27	7:45	*Low	11.6	10.1	17.25	16.89	23.47	9.8	17.30	16.94	23.60
6-28	7:50 A.M.	Ebb	14.6	10.2	17.08	16.73	23.22	9.7	17.12	16.76	23.36
6-28	9:00 P.M.	*Low	13.5	10.0	17.08	16.73	23.24	9.7	17.30	16.94	23.60
6-29	9:30 A.M.	Low	14.6	10.7	17.29	16.93	23.42	9.8	17.18	16.82	23.43
6-29	7:10 P.M.	*Ebb	14.4	10.2	17.27	16.91	23.48	9.9	17.30	16.94	23.57
6-30	11:30 A.M.	*Low	17.0	11.5	16.35	16.02	22.02	10.2	16.68	16.34	22.67
6-30	8:40 P.M.	*Ebb	12.5	10.3	17.15	16.79	23.30	9.8	17.26	16.90	23.54
7-1	12:00 A.M.	Low	19.2	11.9	16.59	16.26	22.28	10.3	16.70	16.36	22.69
7-1	8:35 P.M.	High	12.3	10.4	17.13	16.77	23.20	9.9	17.16	16.80	23.39
7-5	8:00 P.M.	Flood	12.7	10.6	16.96	16.61	22.99	10.7	17.00	16.65	23.04
7-6	10:35 A.M.	Ebb	16.0	11.2	17.09	16.74	23.08	9.9	17.18	16.82	23.40
7-6	8:30 P.M.	Flood	14.2	10.6	17.07	16.72	23.16	9.9	17.21	16.85	23.44

*The difference between the high-low tide and the low-high tide is 60 cm or less.

TABLE 3—Continued.

Date 1927	Time	Tide	Surface				Depth of 12.8 meters				
			Temperature		Chlorinity		Specific gravity σ_t	Tempera- ture water	Chlorinity		Specific gravity σ_t
			Air	Water	Per liter 20°C	Per kilo			Per liter 20°C	Per kilo	
7-24	8:15 A.M.	Flood	17.0	13.7	14.78	14.52	19.53	10.7	15.77	15.47	22.63
7-24	8:30 P.M.	Flood	18.0	14.0	13.82	13.59	18.17	10.7	16.71	16.37	22.63
7-25	9:00 A.M.	Flood	20.5	13.3	14.63	14.37	19.38	11.2	16.32	16.00	22.04
7-25	8:45 P.M.	Flood	15.0	13.0	14.86	14.59	19.76	11.6	16.44	16.11	22.11
7-26	8:50 A.M.	Low	15.5	13.3	15.13	14.85	20.06	11.4	16.29	15.97	21.96
7-26	7:55 P.M.	*Low	14.3	12.2	15.78	15.48	21.13	11.0	16.63	16.29	22.49
7-27	7:10 P.M.	*Ebb	16.2	13.0	15.75	15.45	20.95	10.8	16.75	16.41	22.68
7-28	8:10 A.M.	Ebb	15.5	12.2	16.10	15.79	21.56	10.9	16.75	16.41	22.65
7-28	8:50 P.M.	Ebb	15.5	13.0	16.09	15.78	21.43	10.9	16.80	16.46	22.73
7-31	9:20 A.M.	Ebb	16.0	14.8	16.68	16.34	22.02	10.6	17.09	16.74	23.18
7-31	7:00 P.M.	High	17.0	13.0	16.48	16.15	21.92	11.0	16.81	16.47	22.73
8-1	10:00 A.M.	*Ebb	20.8	12.0	16.66	16.32	22.35	11.0	17.01	16.66	23.06
8-1	7:05 P.M.	High	15.0	12.5	16.39	16.06	21.89	10.6	17.01	16.66	23.06
8-2	8:00 A.M.	*Ebb	14.0	12.0	16.59	16.26	22.26	10.7	17.00	16.65	23.04
8-2	7:20 P.M.	High	14.0	11.2	16.93	16.58	22.85	10.7	17.00	16.65	23.04
8-3	7:55 A.M.	*High	15.0	11.3	16.80	16.46	22.65	10.7	17.12	16.76	23.20
8-3	7:15 P.M.	Flood	14.0	12.2	16.80	16.46	22.49	10.7	17.12	16.76	23.20
8-4	7:55 A.M.	Flood	16.0	11.2	16.86	16.51	22.75	10.8	17.08	16.73	23.13
8-4	7:00 P.M.	Flood	14.9	11.8	16.80	16.46	22.56	11.0	17.00	16.65	22.99
8-5	8:10 A.M.	Flood	13.4	11.5	16.84	16.49	22.67	10.7	17.08	16.73	23.14
8-5	7:30 P.M.	Flood	18.0	15.5	14.17	13.93	18.36	10.8	16.93	16.58	22.92
8-6	8:00 A.M.	Flood	16.0	14.1	14.94	14.67	19.67	11.3	16.74	16.40	22.58
8-6	7:45 P.M.	*Flood	14.2	16.0	13.60	13.38	17.51	11.2	16.81	16.47	22.70

*The difference between the high-low tide and the low-high tide is 60 cm or less.

TABLE 3—Continued.

Date 1927	Time	Tide	Surface				Depth of 12.8 meters				
			Temperature		Chlorinity		Specific gravity σ_t	Tempera- ture water	Chlorinity		Specific gravity σ_t
			Air	Water	Per liter 20°C	Per kilo			Per liter 20°C	Per kilo	
7-7	8:30 A.M.	Flood	14.6	11.0	17.11	16.76	23.15	10.1	17.10	16.75	23.28
7-7	8:30 P.M.	Flood	15.3	11.0	16.96	16.61	22.93	10.1	17.10	16.75	23.28
7-8	9:30 A.M.	Flood	18.6	11.0	17.03	16.68	23.03	10.1	17.14	16.78	23.32
7-8	8:10 P.M.	Flood	16.0	11.0	16.72	16.38	22.60	10.5	16.96	16.61	23.01
7-9	8:40 P.M.	Flood	12.7	11.2	16.23	15.91	21.91	10.7	16.59	16.26	22.47
7-10	10:35 A.M.	Flood	15.9	11.7	16.47	16.14	22.14	10.1	17.03	16.68	23.17
7-10	8:35 P.M.	*Flood	14.9	11.2	16.60	16.27	22.42	10.5	16.84	16.49	22.84
7-11	9:25 A.M.	Flood	16.5	11.6	16.13	15.82	21.71	10.9	16.34	16.01	22.10
7-12	7:55 A.M.	Low	13.7	11.1	16.63	16.29	22.47	10.3	16.88	16.53	22.92
7-12	8:35 P.M.	*Low	11.7	10.5	17.03	16.68	23.11	10.2	17.18	16.82	23.34
7-13	7:55 A.M.	Ebb	12.9	10.9	16.85	16.50	22.78	10.0	17.23	16.87	23.45
7-13	8:20 P.M.	*Low	15.5	10.6	17.30	16.94	23.45	9.9	17.39	17.02	23.69
7-14	A.M.	Low	17.12	16.76	17.17	16.81	...
7-14	8:30 P.M.	*Ebb	13.0	10.1	17.19	16.83	23.38	9.7	17.47	17.10	23.82
7-15	11:35 A.M.	Low	19.8	11.6	17.12	16.76	23.04	10.0	17.27	16.91	23.52
7-15	8:40 P.M.	*Ebb	17.36	16.99	...	9.8	17.43	17.06	23.74
7-17	7:35 P.M.	High	14.7	12.2	17.02	16.67	22.80	10.0	17.34	16.97	23.59
7-19	8:40 P.M.	High	12.2	10.1	17.31	16.95	23.55	10.0	17.35	16.98	23.61
7-20	8:40 P.M.	High	14.0	10.5	17.27	16.91	23.43	10.1	17.31	16.95	23.55
7-21	9:45 A.M.	High	14.0	11.0	17.39	17.02	23.51	10.0	17.38	17.01	23.65
7-21	8:30 P.M.	Flood	12.0	10.5	17.25	16.89	23.40	10.1	17.31	16.95	23.55
7-22	8:45 A.M.	*Flood	13.0	10.8	17.04	16.69	23.08	10.5	17.29	16.93	23.47
7-22	3:15 P.M.	Low	25.5	11.0	17.25	16.89	23.32	10.2	17.37	17.00	23.62

*The difference between the high-low tide and the low-high tide is 60 cm or less.

TABLE 3—Continued.

Date 1927	Time	Tide	Surface				Depth of 12.8 meters			
			Temperature		Chlorinity		Tempera- ture water	Chlorinity		Specific gravity σ_t
			Air	Water	Per liter 20°C	Per kilo		Per liter 20°C	Per kilo	
8-7	9:00 A.M.	Flood	14.0	14.0	14.52	14.27	11.6	16.40	16.07	22.07
8-7	7:30 P.M.	*Flood	14.8	15.2	14.37	14.12	12.7	15.66	15.32	20.84
8-8	8:05 P.M.	*Flood	13.4	14.0	15.31	15.03	12.5	15.98	15.67	21.34
8-9	8:05 A.M.	Low	14.0	14.1	15.08	14.80	13.1	15.60	15.31	20.65
8-10	8:10 A.M.	Low	13.1	13.0	16.08	15.77	11.5	16.60	16.27	22.37
8-11	8:00 A.M.	*Low	14.6	11.8	16.50	16.17	11.5	16.62	16.29	22.40
8-11	8:15 P.M.	*Low	12.9	11.0	17.02	16.67	10.7	17.04	16.69	23.09
8-12	10:30 A.M.	Low	14.0	11.2	16.85	16.50	11.0	16.96	16.61	22.93
8-12	7:20 P.M.	*Ebb	12.4	11.2	17.11	16.76	10.4	17.32	16.96	23.52
8-14	9:05 A.M.	Low	18.2	10.8	17.14	16.78	10.6	17.21	16.85	23.33
8-14	7:00 P.M.	Ebb	16.4	10.5	17.31	16.95	10.4	17.30	16.94	23.49
8-15	8:50 A.M.	Ebb	17.4	10.8	17.24	16.88	10.5	17.26	16.90	23.41
8-15	7:05 P.M.	High	16.6	10.6	17.26	16.90	10.6	17.28	16.92	23.42
8-16	8:10 A.M.	Ebb	15.0	10.8	17.07	16.72	10.5	17.19	16.83	23.32
8-16	6:55 P.M.	High	14.2	10.7	17.20	16.84	10.6	17.27	16.91	23.41
8-17	7:05 P.M.	High	14.0	10.9	17.14	16.78	10.7	17.17	16.81	23.25
8-18	8:05 A.M.	High	13.6	10.8	17.14	16.78	10.7	17.19	16.83	23.30
8-18	7:00 P.M.	Flood	20.1	10.6	17.16	16.80	10.7	17.18	16.82	23.27
8-19	8:00 A.M.	Flood	13.1	10.6	17.20	16.84	10.6	17.22	16.86	23.34
8-19	7:10 P.M.	Flood	13.6	11.0	17.22	16.86	10.7	17.15	16.79	23.22
8-20	8:30 A.M.	Flood	16.1	10.9	17.15	16.79	10.5	17.30	16.94	23.47
8-20	8:00 P.M.	Flood	11.8	10.8	17.09	16.74	11.0	17.18	16.92	23.36

*The difference between the high-low tide and the low-high tide is 60 cm or less.

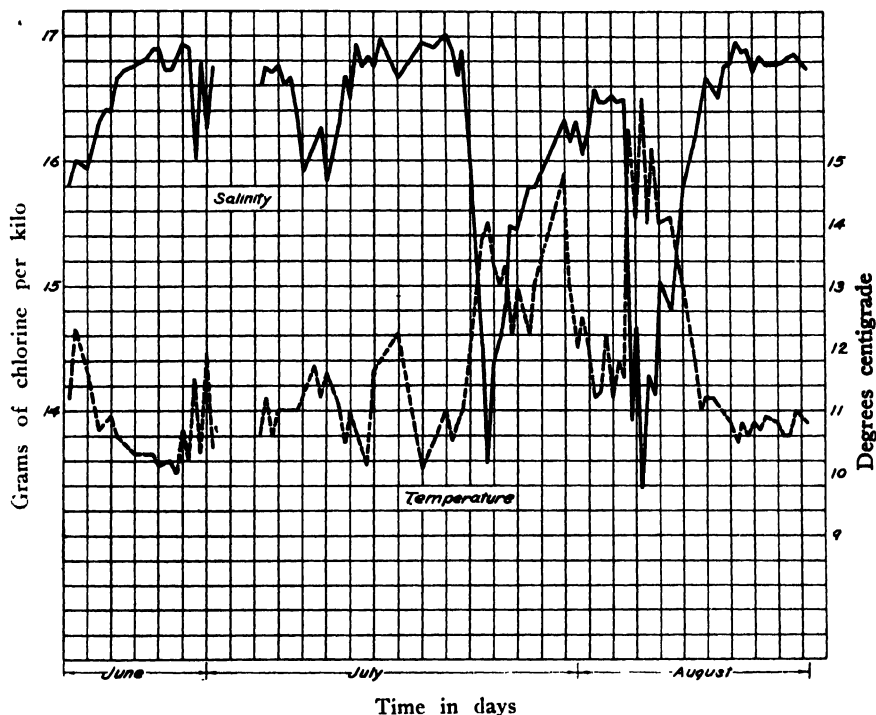


Fig. 2. Daily variation of the surface sea water at the Puget Sound Biological Station.

countered at the bottom of the channel, altho the latter were decidedly abnormal.

3. The lowest observation for the chlorinity varies from the mean by 17.6% at the surface and 6.9% at the bottom. The highest observation varied from the mean by 4.8% at the surface and 2.4% at the bottom.

4. On July 22 normal conditions were observed and yet two days later a very marked drop in chlorinity was noted equivalent to 3.30 ‰ Cl. The changes occurring in the depth samples were very much less, thus indicating that a large volume of fresh water had mixed with the surface layers and was floated and carried along by the flood tide. The sudden decrease in chlorinity was accompanied by a marked increase in temperature of the surface waters but that of the bottom water remained normal. These changes in chlorinity and temperature produced a great variation between the densities of the waters situated at the surface and at the bottom.

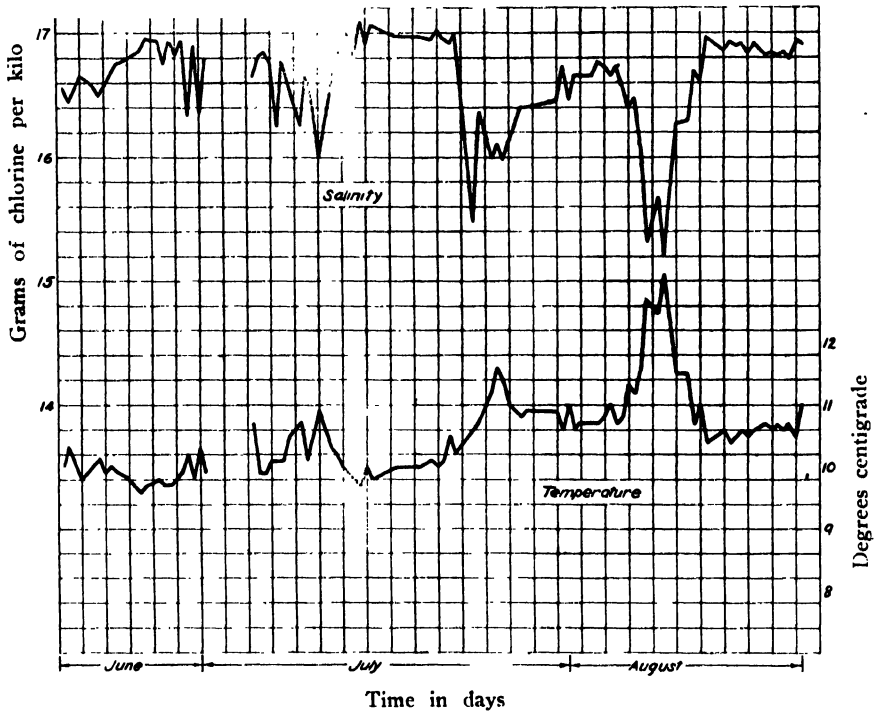


Fig. 3. Daily variation of the sea water at the Puget Sound Biological Station at 12.8 meters.

TABLE 4. Mean and maximum and minimum conditions over a two month period.

	Temperature		Chlorinity		Specific gravity σ_t
	Air °C	Water °C	Per liter 20°C	Per kilo	
Surface					
Maximum.....	25.5	16.0	17.39	17.02	23.55
Minimum.....	11.6	10.0	13.60	13.38	17.51
Difference.....	13.9	6.0	3.79	3.64	6.04
Mean.....	15.4	11.6	16.57	16.24	22.29
Depth 12.8 meters					
Maximum.....		13.1	17.39	17.02	23.67
Minimum.....		9.6	15.77	15.47	20.65
Difference.....		3.5	1.62	1.55	3.02
Mean....		10.5	16.97	16.62	23.80

TABLE 5. *Weekly variations of conditions of sea water over a one year period.*

Date	Time	Tide	Surface			Depth of 12.8 meters		
			Temperature		Specific gravity σ_t	Chlorinity		Specific gravity σ_t
			Air	Water		Per liter 20°C	Per kilo	
9-6-26	10:15 A.M.	Low	25.3	11.4	22.95	17.03	16.68	23.11
9-6-26	5:10 P.M.	High	20.0	11.3	23.43	17.38	17.01	23.42
9-14-26	7:15 P.M.	High	17.16	16.80	...
9-27-26	9:50 A.M.	High	13.8	10.7	23.72	17.52	17.15	24.03
10-12-26	8:45 A.M.	High	10.7	9.6	24.01	17.60	17.22	...
10-19-26	9:00 A.M.	Low	11.1	10.4	23.80	17.54	17.17	23.99
10-19-26	4:45 P.M.	Ebb	14.0	10.4	23.85	17.58	17.20	24.06
10-27-26	11:00 A.M.	Ebb	14.4	10.6	23.52	17.36	16.99	23.60
10-30-26	8:00 A.M.	Flood	13.4	10.3	22.75	16.74	16.40	...
11-2-26	8:50 A.M.	Low	13.5	10.2	23.17	17.04	16.69	23.30
11-3-26	2:00 P.M.	High	15.2	10.4	23.15	17.04	16.69	23.43
11-9-26	9:00 A.M.	High	11.3	9.9	23.69	17.38	17.01	23.94
11-17-26	8:30 A.M.	Low	7.8	9.6	23.82	17.44	17.07	23.96
11-18-26	3:15 P.M.	High	8.6	9.6	23.84	17.46	17.09	23.90
11-24-26	9:00 A.M.	High	11.9	9.7	23.72	17.38	17.01	23.79
12-2-26	2:15 P.M.	High	14.6	9.7	23.85	17.48	17.11	23.90
12-8-26	8:10 A.M.	High	4.8	9.6	23.52	17.23	16.87	23.60
12-8-26	12:45 P.M.	Low	11.4	9.7	23.53	17.25	16.89	23.61
12-16-26	7:35 A.M.	Low	7.7	8.7	23.76	17.30	16.94	23.78
12-16-26	1:35 P.M.	High	8.8	8.9	23.66	17.26	16.90	23.72
12-24-26	9:05 A.M.	High	6.6	8.6	23.80	17.32	16.96	24.03
1-8-27	9:00 A.M.	High	8.1	8.5	23.72	17.26	16.93	23.84
1-8-27	2:55 P.M.	Low	8.2	8.6	23.65	17.22	16.86	23.85
1-14-27	12:35 P.M.	High	8.7	8.3	23.45	17.04	16.69	23.56
1-14-27	8:35 P.M.	Low	7.8	8.3	23.50	17.08	16.73	...

TABLE 5—Continued.

Date	Time	Tide	Surface				Depth of 12.8 meters			
			Temperature		Chlorinity		Tempera- ture water	Chlorinity		Specific gravity σ_t
			Air	Water	Per liter 20°C	Per kilo		Per liter 20°C	Per kilo	
1-21-27	8:00 A.M.	High	-2.6	7.5	17.10	16.75	7.2	17.18	16.82	23.80
1-21-27	1:15 P.M.	Low	0.0	7.6	17.15	16.79	7.2	17.15	16.79	23.75
1-29-27	11:15 A.M.	High	7.9	7.5	17.20	16.84	7.2	17.28	16.92	23.92
1-29-27	8:00 P.M.	Low	2.2	7.6	17.14	16.78	7.2	17.18	16.82	23.80
2-8-27	9:30 A.M.	High	8.1	7.5	17.12	16.76	7.4	17.14	16.78	23.71
2-8-27	4:20 P.M.	Low	8.9	7.8	17.14	16.78	7.4	17.19	16.83	23.78
2-18-27	10:55 A.M.	High	8.9	7.6	17.08	16.73	7.4	17.19	16.83	23.78
2-18-27	12:35 P.M.	Low	10.5	7.7	17.04	16.69	7.4	17.08	16.73	23.63
2-24-27	8:50 A.M.	High	7.6	7.8	17.16	16.80	7.4	17.18	16.82	23.77
2-24-27	4:35 P.M.	Low	10.2	8.1	17.08	16.73	7.5	17.12	16.76	23.67
3-14-27	9:35 A.M.	Low	10.3	8.2	17.09	16.74	7.5	17.12	16.76	23.67
3-19-27	11:15 A.M.	Low	8.7	8.7	17.16	16.80	7.7	17.12	16.76	23.64
3-19-27	5:45 P.M.	High	8.4	8.0	17.18	16.82	7.7	17.20	16.84	23.75
3-26-27	7:30 A.M.	High	7.1	8.1	17.13	16.77	7.7	17.17	16.81	23.71
3-26-27	4:30 P.M.	Low	8.5	8.5	17.01	16.66	7.9	17.08	16.73	23.57
4-2-27	10:40 A.M.	Low	11.2	8.5	17.24	16.88	8.0	17.27	16.91	23.82
4-2-27	5:10 P.M.	High	10.3	8.3	17.33	16.96	7.9	17.32	16.96	23.90
4-8-27	4:00 P.M.	Low	9.5	8.4	17.35	16.98	7.9	17.38	17.01	23.97
4-9-27	9:00 A.M.	High	9.7	8.4	17.38	17.01	7.9	17.38	17.01	23.97
4-19-27	12:15 P.M.	Low	11.5	8.8	17.25	16.89	8.1	17.25	16.89	23.78
4-19-27	7:30 P.M.	High	4.3	8.3	17.26	16.93	8.0	17.29	16.93	23.84
5-4-27	7:25 P.M.	High	9.6	8.7	17.57	17.20	8.3	17.56	17.19	24.16
5-5-27	1:20 P.M.	Low	15.0	9.0	17.49	17.12	8.4	17.50	17.13	24.07
5-12-27	8:50 A.M.	Low	13.1	9.2	17.43	17.06	8.6	17.45	17.08	23.96

TABLE 5—Continued

Date	Time	Tide	Surface				Depth of 12.8 meters			
			Temperature		Chlorinity		Tempera- ture water	Chlorinity		Specific gravity σ_t
			Air	Water	Per liter 20°C	Per kilo		Per liter 20°C	Per kilo	
5-12-27	4:00 P.M.	Ebb	14.9	9.2	17.44	17.07	8.7	17.46	17.09	23.95
5-19-27	8:20 P.M.	High	8.2	9.0	17.40	17.03	8.2	17.35	16.98	23.89
6- 9-27	2:45 P.M.	High	15.5	10.0	17.44	17.07	9.5	17.41	17.04	23.77
6-16-27	11:00 A.M.	Low	16.2	11.0	17.10	16.75	9.7	17.18	16.82	23.43
6-16-27	7:20 P.M.	High	15.2	9.9	17.45	17.08	9.5	17.44	17.07	23.82
6-26-27	8:00 A.M.	Low	13.5	10.3	17.17	16.81	9.6	17.21	16.85	23.50
6-26-27	7:20 P.M.	Low	12.7	10.3	17.25	16.89	9.7	17.33	16.96	23.65
7- 1-27	12:00 A.M.	Low	19.2	11.9	16.59	16.26	10.3	16.70	16.36	22.69
7- 1-27	8:35 P.M.	High	12.3	10.4	17.13	16.77	9.9	17.16	16.80	23.39
7- 6-27	10:35 A.M.	Ebb	16.0	11.2	17.09	16.74	9.9	17.18	16.82	23.40
7- 6-27	8:30 P.M.	Flood	14.2	10.6	17.07	16.72	9.9	17.21	16.85	23.44
7-13-27	7:55 A.M.	Low	12.9	10.9	16.85	16.50	10.0	17.23	16.87	23.45
7-13-27	8:20 P.M.	Low	15.5	10.6	17.30	16.94	9.9	17.39	16.94	23.67
7-21-27	9:45 A.M.	High	14.0	11.0	17.39	17.02	10.0	17.38	17.02	23.67
7-21-27	8:30 P.M.	High	12.0	10.5	17.25	16.89	10.1	17.31	16.95	23.55
7-28-27	8:10 A.M.	Ebb	15.5	12.2	16.10	15.79	10.8	16.75	16.41	22.68
7-28-27	8:50 P.M.	Ebb	15.5	13.0	16.09	15.78	10.9	16.75	16.41	22.65
8- 4-27	7:55 A.M.	Flood	16.0	11.2	16.86	16.51	10.8	17.08	16.73	23.13
8- 4-27	7:00 P.M.	Flood	14.9	11.8	16.80	16.46	11.0	17.00	16.65	22.99
8-11-27	8:00 A.M.	Low	14.6	11.8	16.50	16.17	11.5	16.62	16.29	22.40
8-11-27	8:15 P.M.	Low	12.9	11.0	17.02	16.67	10.7	17.04	16.69	23.09
8-18-27	8:05 A.M.	High	13.6	10.8	17.14	16.78	10.6	17.19	16.83	23.30
8-18-27	7:00 P.M.	High	20.1	10.6	17.16	16.80	10.7	17.18	16.82	23.27
8-26-27	9:50 A.M.	High	14.0	10.5	17.31	16.95	10.5	17.35	16.98	23.53

5. The morning of August 5 showed normal conditions for the flood tide, yet the sample taken in the evening of the same day on the flood tide, gave a decrease of 2.56 ‰ Cl. A change of 4° in the temperature of the surface water was observed while the temperature of the bottom water showed an increase of only 0.1° and a change of only 0.15 ‰ Cl.

6. A still greater drop from the normal was noted on August 6 for the surface water with only a slight variation of the bottom water. From this time until August 11 the chlorinity at the surface was far below normal but there was a general tendency for it to increase while that of the bottom water tended to decrease.

7. High temperatures of the surface waters continued from July 24 to August 11 with only a few exceptions. The bottom water

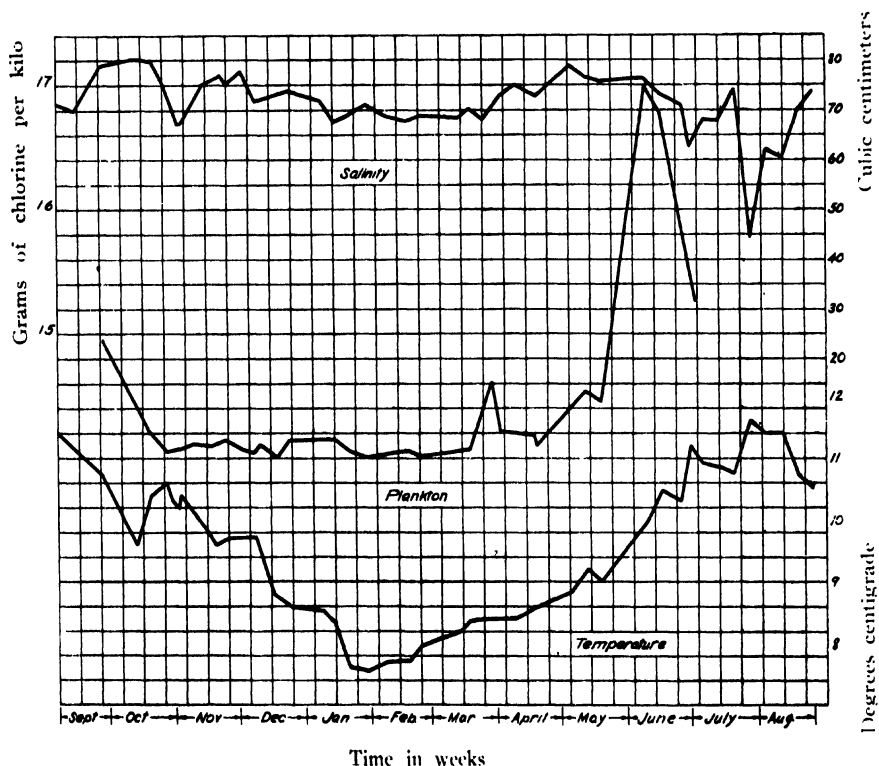


Fig. 4. Weekly variations in the surface sea water at the Puget Sound Biological Station.

did not show any very marked increase in temperature until August 7 and this abnormality only continued for four days.

8. The water at the bottom always showed a higher chlorinity, a greater density and a lower temperature than the surface water.

Weekly Variations

From September 6, 1926 to August 26, 1927 samples of water were taken once or twice a week at the surface and from the bottom of the channel midway between Brown Island and the Puget Sound Biological Station. The data obtained are given in table 5 and graphically shown in figs. 4 and 5. Table 6 gives a summary of the data presented in table 5 by showing the mean and the maximum and minimum conditions obtained during the year. A study of the tables and the graphs discloses the following facts:

1. The maximum temperature for the surface water was obtained on July 28, 1927 while that of the bottom water was observed on August 11, 1927.

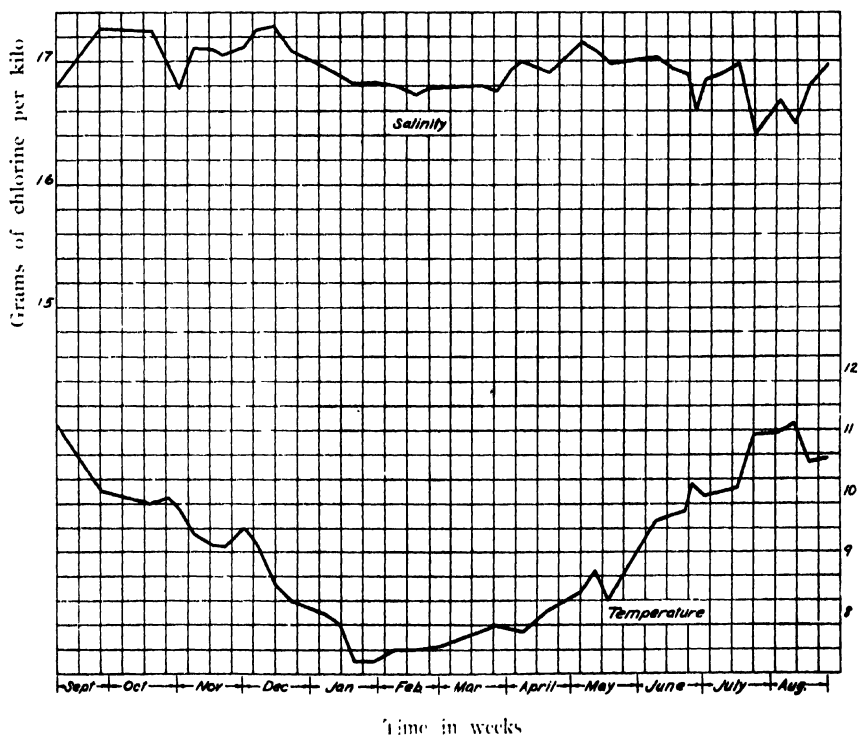


Fig. 5. Weekly variations of the sea water at a depth of 12.8 meters off the Puget Sound Biological Station.

TABLE 6. *Mean and maximum and minimum weekly conditions over a period of one year.*

	Temperature		Chlorinity		Specific gravity σ_t
	Air °C	Water °C	Per liter 20°C	Per kilo	
Surface					
Maximum . . .	25.3	13.0	17.60	17.22	24.12
Minimum . . .	-2.5	7.5	16.09	15.78	21.43
Difference . . .	27.8	5.5	1.51	1.44	2.69
Mean	11.6	9.5	17.19	16.82	23.46
Depth 12.8 meters					
Maximum . . .		11.5	17.66	17.28	24.16
Minimum . . .		7.2	16.62	16.29	22.40
Difference . . .		4.3	1.04	0.99	1.76
Mean		9.1	17.24	16.88	23.62

2. The minimum temperature for the surface water was observed three times from January 21, 1927 to February 8, 1927. The minimum temperature was observed four times for the depth samples on January 21 and 29.

3. The maximum chlorinity for the surface occurred on October 12, 1926 while the minimum was recorded on July 28, 1927. The maximum and minimum for the bottom waters were observed on September 27 and October 19, 1926 for the former and on August 11, 1927 for the latter.

4. The maximum densities were secured both for the surface and bottom samples on April 4, 1927, the minimum on July 28 for the surface and on August 11, 1927 for the bottom.

5. In general there is a rather definite relation between the temperature of the water and that of the atmosphere.

6. Lower chlorinities were generally obtained at low tide or during ebbing conditions.

7. The highest chlorinities occurred in the fall and the spring while the lowest ones were recorded during the summer.

8. The chlorinity and the actual density was always greater for the bottom waters than for those of the surface.

9. The greatest stratification of the waters occurred during the periods of low chlorinity and high temperature.

10. The lowest observation for the chlorinity varied from the mean by 6.2% at the surface and 3.5% at the bottom, while the

highest observation varied from the mean by 2.4% for both the surface and bottom water.

DISCUSSION

The waters of the Puget Sound Biological Station show a variation of conditions that is relatively small from hour to hour but over a longer period of time the changes may become very marked. Such changes occur primarily in the surface water and from the data presented above, it might be concluded that the water in the deeper

TABLE 7. *Monthly rainfall and chlorinity.*

Month 1926	Rainfall inches	Mean chlorin- ity, ‰ Cl	Mean water temperature
September.....	1.17	16.91	11.2
October.....	2.91	17.00	10.3
November.....	3.19	16.93	9.9
December.....	4.39	16.95	9.2
1927			
January.....	3.21	16.79	8.0
February.....	2.12	16.75	7.8
March.....	2.32	16.76	8.3
April.....	2.22	16.94	8.4
May.....	0.98	17.09	9.0
June.....	0.37	16.92	10.3
July.....	0.52	16.54	11.2
August.....	2.21	16.62	11.1

parts of the San Juan Archipelago undergo only very slight seasonal changes in chlorinity.

In table 7 is given the rainfall at Olga, Orcas Island, month by month from September 1926 to August 1927. From the data in table 5 the average ‰ Cl and temperature for each month was calculated for the surface water and such data are given in the last two columns of table 7. The temperature appears to vary inversely as the rainfall.

The marked decrease in chlorinity obtained at certain periods was undoubtedly caused by the inflow of fresh water from the Fraser River and to a very much lesser degree by the Skagit River. The abnormalities result from freshets, and strong winds and extreme tides which force the diluted waters accumulating in the Gulf of Georgia into the tidal currents bathing the San Juan Archipelago.

Data collected by the Department of the Interior of the Dominion Water Power Branch and supplied to the authors thru Dr. W. A. Clemens, Director of the Pacific Biological Station at Nanaimo, British Columbia, show the following facts concerning the discharge of the Fraser River.

Beginning April 15, 1927, there was a discharge of 17,400 second feet which gradually increased to 97,300 second feet on May 13, 1927. After this date there was a very rapid increase which reached a maximum of 306,000 second feet on June 14, 1927. From the latter date to August 31, 1927, there was a steady decrease when a flow of 97,300 second feet was recorded. Thus freshet conditions of the

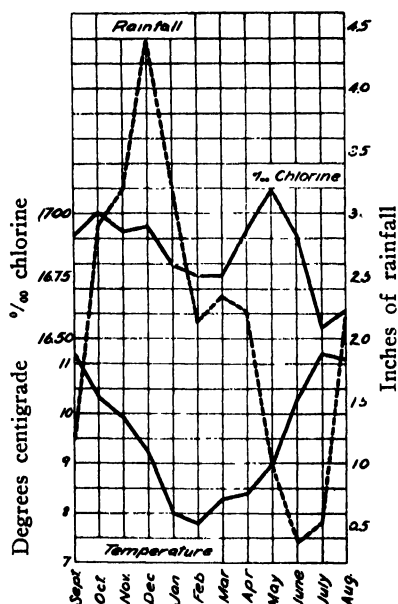


Fig. 6. Relation of temperature and chlorinity to the rainfall.

Fraser River may be said to extend from May thru to August, the maximum being reached in June. This great volume of fresh water flowing into the Gulf of Georgia has an effect upon the waters of the Biological Station when there are proper meteorological and tidal conditions (Lucas and Hutchinson, 1928).

The average discharge of the Skagit River at Sedro Woolley is 16,100 second feet.

OBSERVATIONS ON PLANKTON³

When the samples of water for the study of the weekly variations of the conditions were collected, plankton tows were also made at the surface. The length of each tow was approximately 200 meters and was made with a No. 20 surface-tow plankton net having a diameter of 9 inches. The plankton was removed from the net and then treated with a four per cent formaldehyde solution and eventually transferred to 100 ml. graduated tubes. After settling for eighteen hours, the volume of the plankton was noted. Table 8 gives a summary of the data thus obtained while the relation between the plankton and chlorinity are shown in figure 4.

TABLE 8. *Volume of plankton obtained in surface tows of two hundred meters' length, September, 1926, to July, 1927.*

Date	Volume ml	Remarks
Sept. 27	24.0	Phytoplankton predominant, chiefly filamentous diatoms
Oct. 19	5.5	Phytoplankton predominant, chiefly filamentous diatoms
Oct. 27	1.5	Phytoplankton predominant, filamentous forms decreasing
Nov. 2	2.0	Phytoplankton predominant, chiefly <i>Coscinodiscus</i> species
Nov. 9	3.0	Phytoplankton predominant, chiefly <i>Coscinodiscus</i> species
Nov. 17	2.5	Phytoplankton predominant, chiefly <i>Coscinodiscus</i> species
Nov. 24	3.8	Phytoplankton predominant, chiefly <i>Coscinodiscus</i> species
Dec. 2	1.7	Phytoplankton predominant, chiefly <i>Coscinodiscus</i> species
Dec. 7	1.0	Phytoplankton and zooplankton about equal
Dec. 8	2.8	Phytoplankton and zooplankton about equal
Dec. 16	0.2	Phytoplankton and zooplankton about equal
Dec. 24	3.6	Phytoplankton slightly predominant (<i>Coscinodiscus</i>)
Jan. 14	4.0	Zooplankton predominant (chiefly due to swarm of small amphipods)
Jan. 21	1.5	Phytoplankton and zooplankton about equal
Jan. 29	0.15	Phytoplankton predominant, chiefly <i>Coscinodiscus</i>
Feb. 8	1.0	Phytoplankton predominant, chiefly <i>Coscinodiscus</i>
Feb. 18	1.5	Phytoplankton and zooplankton about equal
Feb. 24	0.3	Phytoplankton predominant, chiefly <i>Coscinodiscus</i>
Mar. 19	1.9	Zooplankton predominant
Mar. 29	15.1	Phytoplankton markedly predominant, chiefly <i>Thalassiosira</i>
Apr. 2	5.3	Phytoplankton markedly predominant, chiefly <i>Thalassiosira</i>
Apr. 18	4.5	Zooplankton predominant
Apr. 19	2.5	Zooplankton predominant, very few diatoms
May 12	13.5	Zooplankton predominant
May 19	11.5	Zooplankton predominant
June 9	75.0	Phytoplankton markedly predominant, particularly filamentous diatoms
June 16	69.0	Phytoplankton predominant
July 2	31.5	Phytoplankton predominant (diatoms decreasing, zooplankton increasing)

³ The authors wish to acknowledge the aid of Prof. Robert C. Miller, Department of Zoology, University of Washington, in the preparation of much of this portion of the paper.

In addition to the data set forth in the table, the following generalizations in regard to the plankton may tentatively be made:

During the period from the end of October to the end of March, *Coscinodiscus* is the most constant and characteristic diatom; thereafter it drops off somewhat, but never disappears entirely.

At the time when the volumes of the plankton are greatest (Sept. 27, March 29, June 9 and 16), the bulk is made up of filamentous diatoms (*Chaetoceras*, *Thalassiosira*, etc.); these predominate numerically, of course, but not so markedly as the figures would indicate, since the filamentous forms occupy a disproportionately large volume on sedimentation.

Of the zooplankton, the Copepoda constitute the most constant and characteristic forms, both larvae and adults being found in every month. They are least numerous from December 2 to 16, and most numerous (relatively, if not absolutely) from April 18 to May 12.

Of the dinoflagellates, *Ceratium* is most numerous from September 27 to November 17, and falls off practically to zero after February 8. A few were observed on April 2 and March 19, but none thereafter. *Peridinium* was common from September 27 to November 17, disappeared from December 8 to March 29, and thereafter was fairly common to and including July 2.

Noctiluca, occasional in November and December, reappeared on April 2, was abundant on June 9 and 16, and fairly numerous on July 2.

SUMMARY

1. Until data have been collected over a period of years, no general conclusions can be drawn regarding the variation in the physical and chemical conditions of the sea water at the Puget Sound Biological Station.

2. Differences of 1.4°C in temperature, 0.35‰ in chlorinity and 0.49 σ_t (actual density) were observed in hourly tests of surface water during a complete tidal cycle in August 1927.

3. The waters of the Gulf of Georgia diluted by freshet conditions of the Fraser River during the summer months have a marked effect upon the surface waters bathing the San Juan Archipelago. The greatest changes resulting from this condition occurred during the latter part of July and the first part of August.

4. During a two month period in the summer when daily tests were made, variations of 6.0°C, 3.64‰ Cl and 6.04 σ_t were observed

for the surface water, while at a depth of 12.8 meters variations of 3.5°C, 1.55% Cl and 2.03 σ_t were noted.

5. Samples taken once a week thruout one year showed variations of 5.5°C, 1.44% Cl and 2.69 σ_t for the surface water and 4.3°C, 0.99% Cl and 1.76 σ_t for the water at a depth of 12.8 meters. However, if the weekly tests for July and August were omitted, the differences for the surface water would then be 3.9°C, 0.54% Cl and 1.37 σ_t and for the water at 12.8 meters, 3.9°C, 0.57% Cl and 1.05 σ_t .

6. A very marked increase in plankton was noted during the spring and summer months.

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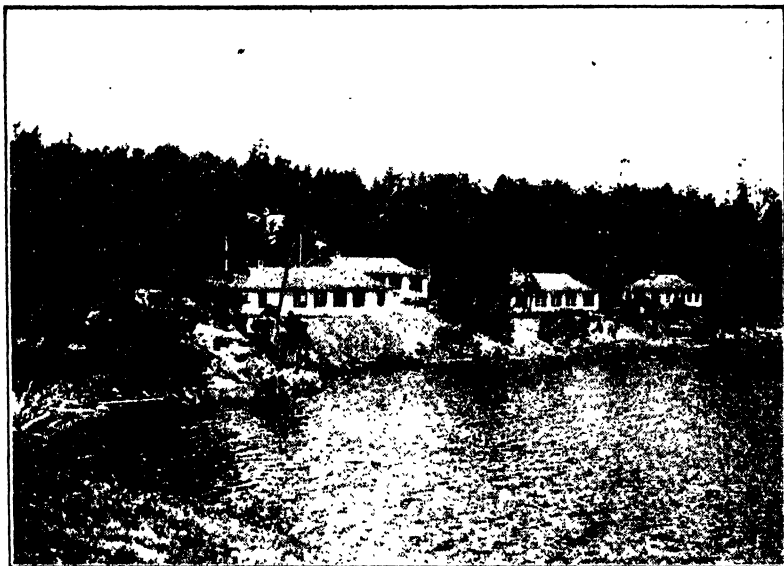
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